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NUMERICAL SIMULATION OF BAY-SHELF EXCHANGES WITH A ONE-DIMENSIONAL MODEL

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ABSTRACT

Hourly water levels, collected over a 610-day period from November 1973 to July 1975 on the Gulf coast of Texas, are used in a numerical model to simulate bay-shelf and inter-bay exchanges over time scales ranging from several hours to several months. A one-dimensional, barotropic model describes open-channel flow in response to a slope in the free surface, with accelerations resisted by a quadratic friction term. The model calculates the accumulation of Gulf water in Corpus Christi Bay, as well as the transport of Gulf water through the bay and into three adjacent sub-estuaries. Time-dependent mixing is incorporated into the calculations by assuming that 15% of the Gulf water entering Corpus Christi Bay during any given hour is retained in the bay. Model results suggest that 50% of the volume of Corpus Christi Bay is replaced within a time period of 105 days. Calculations are repeated using purely tidal forcing of bay-shelf exchanges, and then with a time series from which tidal and higher frequencies have been filtered numerically. Results indicate that the half-life of bay water associated with tidal flushing alone is 122 days; for low-frequency flushing, the half-life increases to 339 days. Repetitive simulations with alternate mixing rates suggest that the true half-life of Corpus Christi Bay water does not differ from the calculated value by more than a few weeks.

Accepted 23 April 1985

INTRODUCTION

Computer models that simulate the exchange of water between estuaries and the adjacent continental shelf are useful tools, both in water quality studies and in ecological studies, because of the effect transport processes have in ferrying suspended and dissolved materials, and planktonic forms of life back and forth from the inner shelf to estuarine nursery areas. Exchanges occur in response to a variety of often unrelated forces and over a wide range of time scales. Of particular importance are the tidal exchanges which are semi-diurnal and diurnal, and meteorologically-forced exchanges which characteristically occur over time scales on the order of one to two weeks.

Forcing mechanisms result in a transport of water to and/or from an estuary in two basic forms: the one-way flow of fresh water through an estuary, and the two-way exchange in response to water level variations along the coast. The relative importance of freshwater outflow and of tidal and nontidal "pumping" in flushing an estuary depends upon tidal conditions along the coast, and upon weather conditions affecting both the coastal zone and the drainage basin supplying the estuary in question. In this sense, one estuary is usually distinctly different from another.

The appropriate analytical approach to quantify exchanges depends upon the complexity of the physical setting and upon the questions being asked in a particular study. Many of the earlier studies involved the concept of the tidal prism, defined as the gain of water between the low and high tide extremes. Ketchum (1951) modified the tidal prism method by segmenting the estuary and assuming complete mixing only within each segment. More recently, Brown and Arellano (1980) introduced a mixing parameter and applied it to a branching estuary. Smith (1982) described tidal flushing of Corpus Christi Bay, along the central Texas Gulf coast, but the tidal prism concept was compromised by replacing the two dominant diurnal constituents with a single hypothetical constituent which was selected to have the same long-term flushing effect. Ancillary data, however, suggested that the exchange of Gulf and bay water did not result from tidal forcing alone. Rather, it was concluded that the ebb and flood of the tide provided a baseline flushing value which could be supplemented in any of several ways. Therefore, in that setting, low-frequency exchanges had to be investigated as well if flushing rates and residence times were to be determined accurately.

Corpus Christi Bay has been the focal point for a series of physical and hydrologic studies over the past 15 years, and a substantial data base is available from individual investigations to analyze and quantify flushing mechanisms. The tidal prisms associated with the K_1 and O_1 constituents are approximately 21 and 25 million cubic meters, respectively (Smith 1977). Tidal flushing alone was estimated to renew 50% of the volume of the bay in approximately 250 tidal cycles (Smith 1982). Quasi-periodic, meteorologically forced exchanges are more difficult to quantify, but the available data suggest that discrete events, occurring over time scales on the order of one to two weeks, can fill or drain as much as 5–10% of the mean low tide volume of the bay. Inverse barometric forcing alone is approximately equal in importance to the M_2 tidal constituent (Smith 1979).

Freshwater run-off events can also be important. Discharge from the Nueces River is sufficient to maintain bay salinities at approximately 26 parts per thousand (Holland *et al.* 1974, 1975). Diener (1975) reported the mean discharge to be 20.6 m^3/s during the period 1951–1968, however the year-to-year variation, and especially the month-to-month variation, can be considerable. Using the multi-annual mean value for fresh-water discharge, and incorporating representative evaporation rates, Smith (1982) calculated

that 856 days would be needed to displace 50% of the low-tide volume of the bay. The tentative conclusion was that apart from run-off events involving discharges considerably greater than the mean, the flow of fresh water through the bay was of secondary importance in maintaining water quality. Hydrographic data compiled by Armstrong (1982) suggest a residence time of approximately 170 days in the estuarine system which includes Corpus Christi Bay. This value reflects the combined effects of both tidal and low-frequency exchanges, but the relative importance of tidal and long-period flushing are as poorly understood for this estuarine system as for most others.

The purpose of this paper is to describe a numerical modeling study designed to investigate and quantify the relative importance of tidal and low-frequency inter-bay and bay-shelf exchanges. This study extends the earlier work (Smith 1982) by including nontidal processes, but the scope is not extended to include the movement of freshwater through the bays. A one-dimensional model is described which suggests that the bay-shelf barotropic pressure gradient is the only significant force driving tidal and low-frequency flushing. Time-dependent mixing quantifies the amount of Gulf water imported into and through Corpus Christi Bay. Comparison of Gulf water retained in the bay with the volume of the bay results in estimates of the flushing rates in response to both tidal and nontidal forcing. In view of the relatively small amount of field data needed to make the calculations and verify the results, the approach described here constitutes a simplified alternative to many other techniques for estimating estuarine flushing.

THE DATA

A collection of water level records from coastal and estuarine tide gauges provided the data base required to calculate bay-shelf and inter-bay exchanges, and to verify the results. Analog water level records from a 610-day period of time (November 15, 1973 through July 17, 1975) at the Aransas Pass (Fig. 1) traced the rise and fall of sea level along the inner shelf of the northwestern Gulf of Mexico. This represented the driving force for bay-shelf exchanges. Values in this and all other time series were read to the nearest 3 mm (±0.01 foot). Some of the high frequency noise in the records was ignored and thus removed as the data were being digitized.

Several shorter water level records were used to verify model calculations. Water level recorders at three locations surrounding Corpus Christi Bay (Stations A, B and C in Fig. 1) were used to compute hour-by-hour variations in the volume of the bay during a 49-day period from January 19 through March 12, 1972 (see Smith 1977), and these volumes were compared with simulated values.

Water level data from the 49-day period were used to verify exchanges between Corpus Christi Bay and Nueces Bay. The analog record from the northwest side of Corpus Christi Bay (Station A in Fig. 1) was used to drive the model, flooding and draining Nueces Bay. A second water level record, from the approximate midpoint of Nueces Bay, was used to estimate its volume. Water level data from this time period were not available for Laguna Madre. A one-year time series from 1974 (Smith 1978), however, was used to calibrate the model on the basis of its ability to reproduce tidal period water level variations observed at the northern extreme of the lagoon.

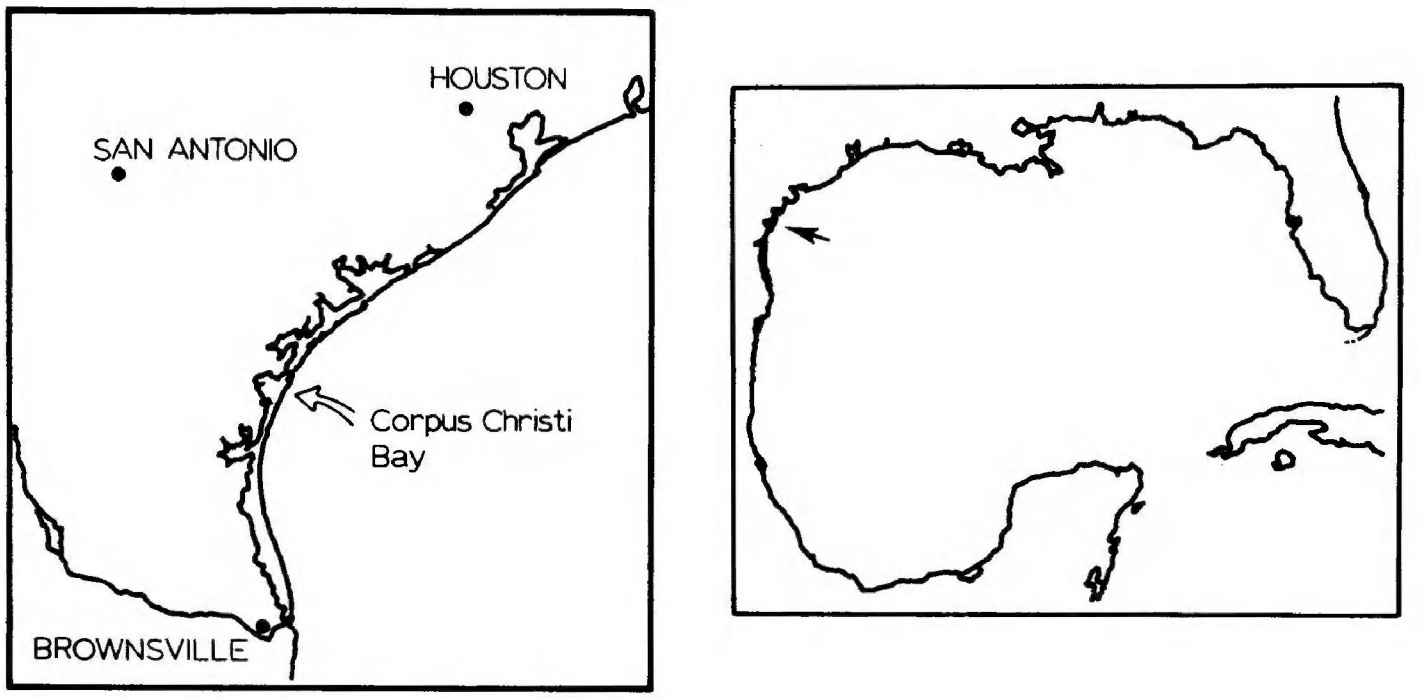

FIG. 1. Map showing locations of water level recorders at Aransas Pass and around Corpus Christi Bay. Insert shows the study area in the northwestern Gulf of Mexico. Stations A, B and C were used to calculate temporal changes in the volume of Corpus Christi Bay; that time series was then used to calibrate the model results.

THE ONE-DIMENSIONAL MODEL

The physical system represented by the model is conceptually similar to that described in detail by Mehta (1978). In the case of Corpus Christi Bay, however, the analog water level record used to drive the calculations reflects both tidal and nontidal forcing, and the tidal component is dominated by two principal diurnal tidal constituents. Also, inter-bay exchanges (see Fig. 1) must be considered along with bay-shelf exchanges if the system is to be modeled realistically.

The equation of motion for the acceleration of water along the channel connecting Corpus Christi Bay with the inner shelf waters of the Gulf of Mexico, and between Corpus Christi Bay and adjacent intracoastal bays, can be expressed in finite difference form as

$$\Delta U/\Delta t = -\alpha\,\Delta p/\Delta x - F\,U\,|\,U\,|,$$

where U is the mean current speed in the long-channel direction averaged over the cross-sectional area of the channel, α is the specific volume of the water, $\Delta p/\Delta x$ is the pressure gradient in the long-channel direction, and F is a measure of frictional retardation which is related to the dimensions and bottom roughness of the channel. Using the hydrostatic equation, the equation of motion may be rewritten in terms of the long-channel slope in the free surface:

$$\Delta U/\Delta t = -g\Delta\eta/\Delta x - F\,U\,|\,U\,|.$$

This form is preferred, because the long-channel slope can be monitored and confirmed using analog water level records.

The frictional resistance to channel flow has been treated analytically in many ways. Wang (1979) expressed friction as proportional to the volume transport, while Bowden (1953) and Hunter (1975) incorporated a frictional deceleration term proportional to the current speed. Mehta (1978) used a channel friction term which was proportional to the Darcy-Weisbach friction factor, and inversely proportional to the mean cross-sectional depth. Here, the frictional force was assumed to be proportional to the square of the cross-sectionally averaged current speed.

The frictional resistance to long-channel flow should be a function of the length of the channel, the cross-sectional area and the bottom roughness. In practice, both bottom roughness and perhaps the cross-sectional area can vary substantially in the long-channel direction. The channel connecting Corpus Christi Bay with the northwestern Gulf of Mexico is not continuously bounded on either side near the entrance to the bay. Spoil islands along the south side of the channel are separated by natural cuts which open directly into the bay (see Fig. 1). Information is not available on spatial variations of bottom roughness along the channel. Thus, in this study, all factors contributing to the frictional retardation of bay-shelf exchanges were combined into a proportionality factor, F. To be dimensionally correct, F must have units of m^{-1} when current speeds are expressed in m/sec. This can be attained from the quotient of a bottom roughness length divided by a cross-sectional area, for example; but the approach used here has been to work with a single number, determined empirically, until the characteristics of frictional retardation in this physical setting can be explored in greater detail.

A series of computer simulations was carried out to verify the model calculations of exchanges between Corpus Christi Bay and the inner shelf of the Gulf of Mexico, and between Corpus Christi Bay and each of the three adjacent sub-estuaries. Individual inter-bay exchanges were verified first. Then the time variation of the volume of Corpus Christi Bay, reflecting both inter-bay and bay-Gulf exchanges, was compared with simulated values, using the multi-bay version of the model. Exchanges between Corpus Christi Bay and Nueces Bay were quantified, with water level data from the northwest shore of Corpus Christi Bay and from the middle of Nueces Bay representing the cause and the effect, respectively. The correlation coefficient calculated from simulated and estimated bay volumes reached a maximum value of +0.875 when $3.06 \times 10^{-5}\ m^{-1}$ was selected for the frictional term. Water level data were not available to verify exchanges between Corpus Christi Bay and Oso Bay. A frictional term value of $3.06 \times 10^{-6}\ m^{-1}$ was selected on the basis of the relatively restricted opening at the mouth of Oso Bay compared to the entrance to Nueces Bay (see Fig. 1).

Exchanges between Corpus Christi Bay and Laguna Madre were verified using water level data recorded along the southern shore of Corpus Christi Bay (Station C). The frictional term resisting exchanges along the channel connecting these two bodies of water was selected to be $1.22 \times 10^{-4}\ m^{-1}$ on the basis of the model's ability to reproduce tidal period water level variations at the northern extreme of Laguna Madre (Smith 1978). A difficulty in the case of Laguna Madre was the unknown rate of decay of the tidal wave form moving southward into the lagoon, and the appropriate surface area of the lagoon—whether or not to include Baffin Bay at the far end of Laguna Madre. In the simulations that followed, the area for Laguna Madre north

of 27°N suggested by Collier and Hedgpeth (1950) was used. This did not include Baffin Bay, even though the exchange of water between Laguna Madre and Baffin Bay was unrestricted. The treatment of the exchange of water between Corpus Christi Bay and Laguna Madre, and the low-frequency movement of water through Laguna Madre are subjects requiring closer inspection in follow-up studies.

Once all inter-bay exchanges had been considered and verified, bay-shelf exchanges were simulated and compared with observations over the 49-day period noted above. Hourly volumes for Corpus Christi Bay were calculated from water level records obtained at three locations around the bay (Fig. 1). The approach used has been described in a previous paper (Smith 1977). Again, the frictional resistance was adjusted until simulated volumes matched observations most closely. The correlation coefficient of these two time series reached a maximum value of +0.976 when a value of $1.43 \times 10^{-4}\ m^{-1}$ was used. It is of interest to compare this value with that which one obtains from the Manning equation, where the proportionality factor in the friction term is given by the Manning coefficient, n, divided by the hydraulic radius, R, raised to the 4/3 power. Using $n = 0.020$ (McDowell and O'Connor 1977), and estimating the cross-sectional area and wetted perimeter of the channel from navigational charts, one obtains a proportionality factor of approximately $1.6 \times 10^{-5}\ m^{-1}$. This is roughly an order of magnitude smaller, but in view of channel irregularities it may not be surprising. Given the fact that a value of 1.43×10^{-4} yielded the best results, this value was carried through the analysis.

The 610-day simulation began with the model bays and shelf assigned the same water level, and thus with no flow. Initial conditions defined water in Corpus Christi Bay, for example, as "Corpus Christi Bay water" regardless of its pre-simulation period history in adjacent bays and in the Gulf. Hourly water levels from Aransas Pass were then used to define the bay-shelf water level difference. The acceleration of channel water resulting from the barotropic pressure gradient force was combined with the cross-sectional area of the channel to determine the volume added to or removed from Corpus Christi Bay. This in turn, created an inter-bay water level difference which produced similar, inter-bay exchanges. In this study, ten-minute time steps were used in the calculations. Channel current speeds for any ten-minute time increment were used to evaluate the frictional resistance to accelerations over the subsequent time increment.

Field observations were not available to estimate a mixing rate, so a value of 15% per hour was used in the simulations for inter-bay exchanges. Hand calculations indicated that a mixing rate of 15% per hour contributed approximately 50% of the Gulf water entering Corpus Christi Bay on an average flood tide. Fifty percent seemed a logical compromise between total mixing and no mixing, until *in situ* data suggest a better value. It is important to note that the mixing rates used for bay-shelf and inter-bay exchanges quantify both turbulent mixing at the interface of two distinct types of water, and the retention of arriving water which becomes entrained and "pinched off" by the internal circulation of the receiving body of water. In the case of bay water ebbing through Aransas pass and onto the inner shelf, the longshore flow was assumed to be more effective in preventing the return of bay water at the start of the following flood. Thus a mixing rate of 20% per hour was used.

Following each calculation of bay-shelf and inter-bay exchanges, the new composition of water was determined for each bay. Flushing, in this study, was defined specifically as the renewal, or repacement by Gulf water of water originally residing in a given bay.

RESULTS

Fig. 2 shows the time variation of volumes simulated by the model for Corpus Christi Bay. Values given on the vertical axis are those relative to the mean low tide volume of the bay; Collier and Hedgpeth (1950) have estimated the volume of the bay at mean low water as $1.113 \times 10^9 m^3$. Temporal variations reflect the net gains and losses resulting from both exchanges between Corpus Christi Bay and the Gulf of Mexico, and between

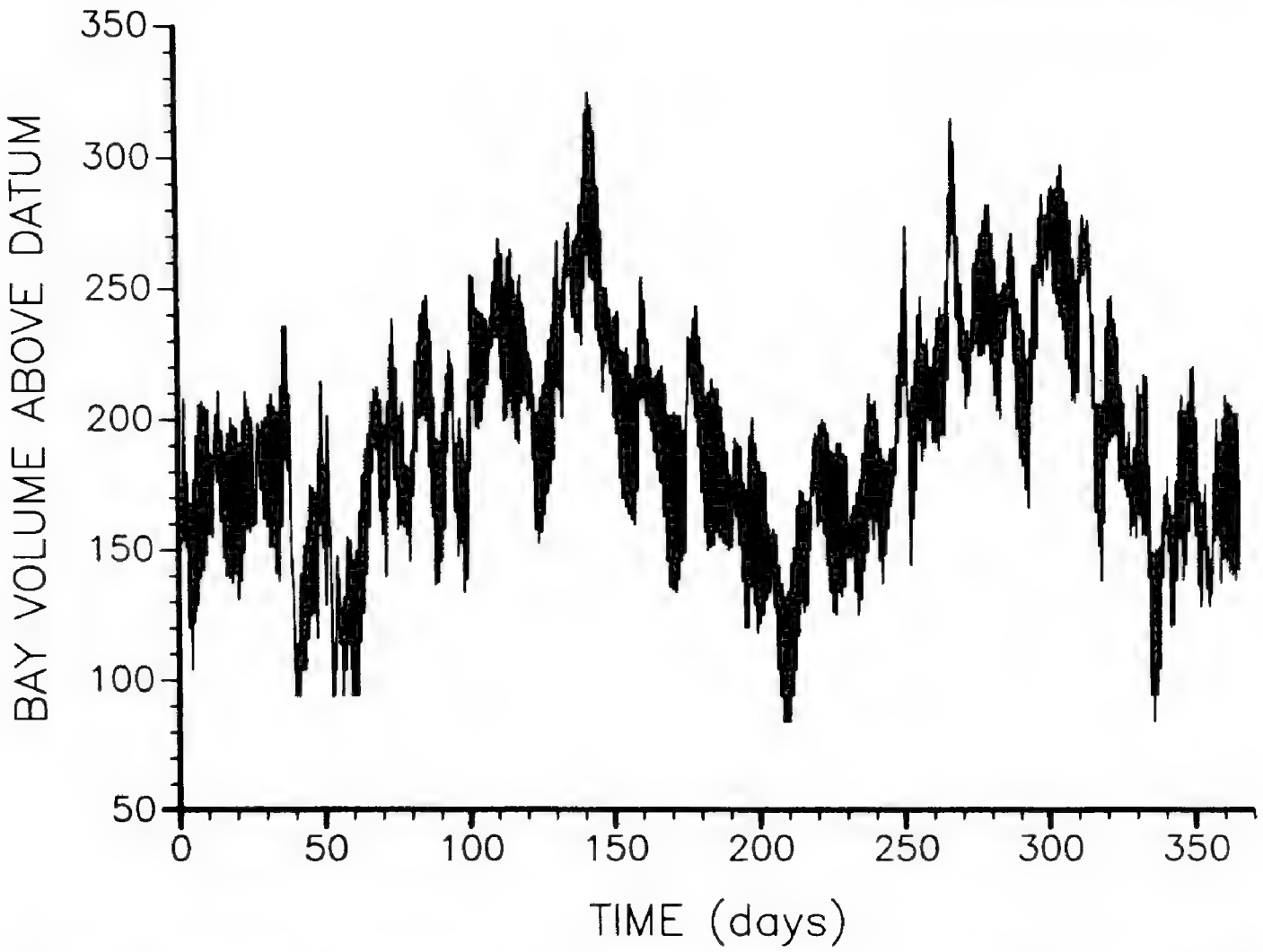

FIG. 2. Computed time variation of the volume of Corpus Christi Bay, 13 November, 1973 through 15 July, 1975. Values are relative to a datum of mean low water.

Corpus Christi Bay and the three adjacent bays. It is important to note that this figure depicts only the exchanges in response to coastal water level fluctuations. The movement of fresh water through the system is not considered except insofar as it might affect the coastal sea level record. The very low-frequency, semi-annual increase and decrease in volume associated with the similar rise and fall in sea level at the coast (Smith 1978) is a prominent feature of the plot. Superimposed onto this seasonal fluctuation, however, are the low-frequency variations occurring in response to meteorological forcing over time scales on the order of one to two weeks. Rapid and erratic changes in volume appear throughout the plot. Over still shorter time scales are the volume changes associated with the dominant diurnal tidal constituents. The once per fortnight beat frequency, as the K_1 and O_1 constituents cycle in and out of phase, is apparent throughout the plot.

Model calculations indicate that the long-term *gross* import of Gulf water into Corpus Christi Bay averages 21.3 million cubic meters per day. But the central issue in this investigation is the flushing of the bay, and to quantify flushing, one must determine the *net* gain of Gulf water over any given tidal cycle. This is computed from the volume of Gulf water which enters on the flood and is mixed or entrained into the bay, minus the loss on the following ebb of previously accumulated Gulf water.

Results are shown in Fig. 3. Because of the greatly compressed time scale,

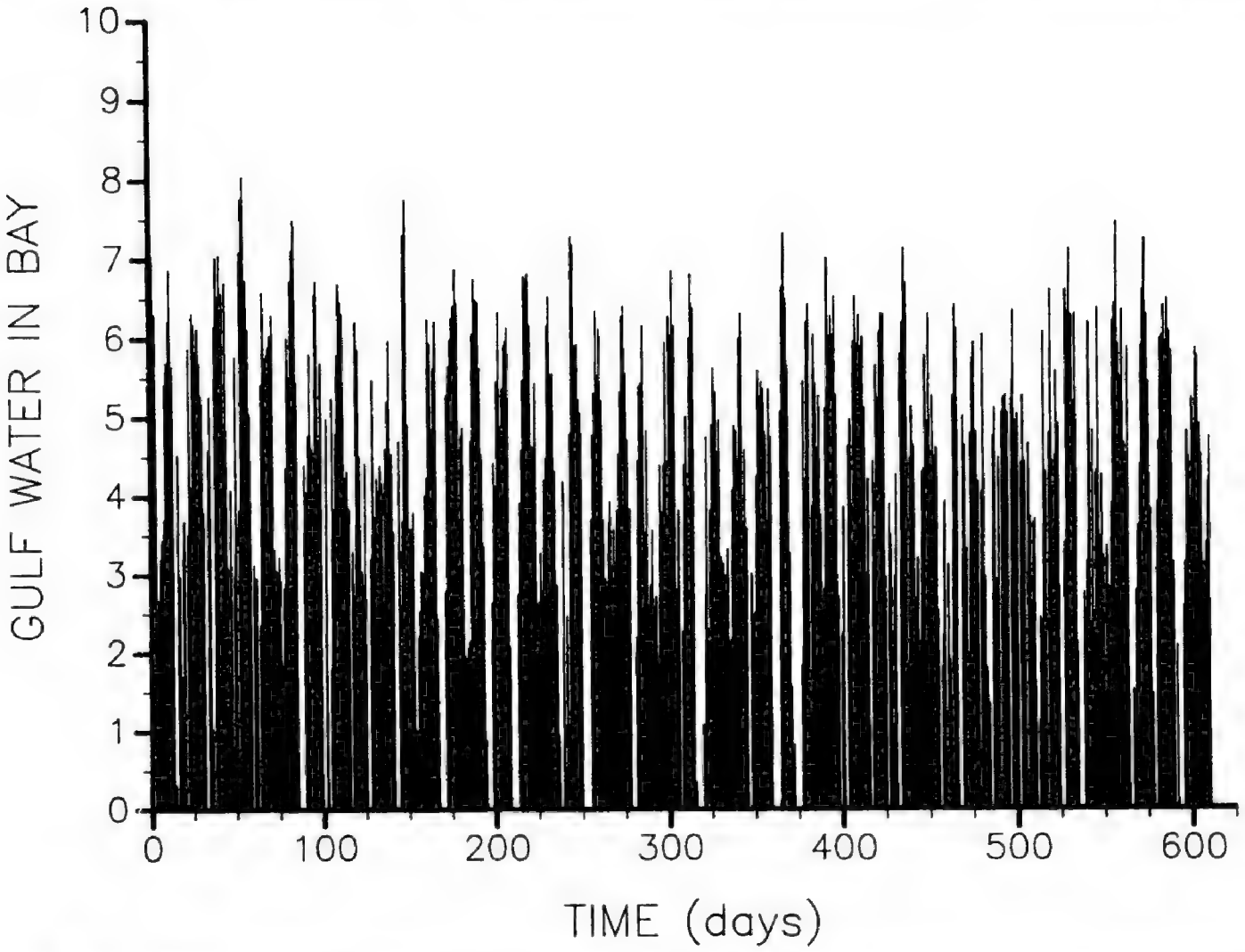

FIG. 3. Influx of Gulf water to Corpus Christi Bay during the 610-day study period (13 November, 1973 through 15 July, 1975. Calculations were based upon an assumed mixing rate of 15% per hour.

individual tidal cycles appear as single vertical lines. The length of any given line indicates only the maximum hourly volume of Gulf water entering the bay, but the plot contains information useful for characterizing how Gulf water is brought into the bay. Particularly noteworthy is the intermittent nature of the gain of Gulf water. Gulf water is injected into the bay at rates of up to 7–8 million cubic meters per hour on most flood tide cycles. Fig. 3 shows that there may be periods lasting several tidal cycles during which no Gulf water is added to the bay. This occurs at times of significant nontidal outflow (Smith 1974), or during times of equatorial tides. Smith (1982) estimated that the channel connecting the bay with the Gulf contains 37.3 million cubic meters of water. At times of equatorial tides, the gain and loss of water for Corpus Christi Bay on the flood and ebb tide is not sufficient to displace the volume temporarily stored in the channel. Thus, Gulf and bay water move back and forth through some fraction of the channel until the K_1 and O_1 constituents cycle back into phase and produce an additive effect.

The fraction of bay water replaced with Gulf water has been quantified in three ways and is represented by the three curves shown in Fig. 4. Initially,

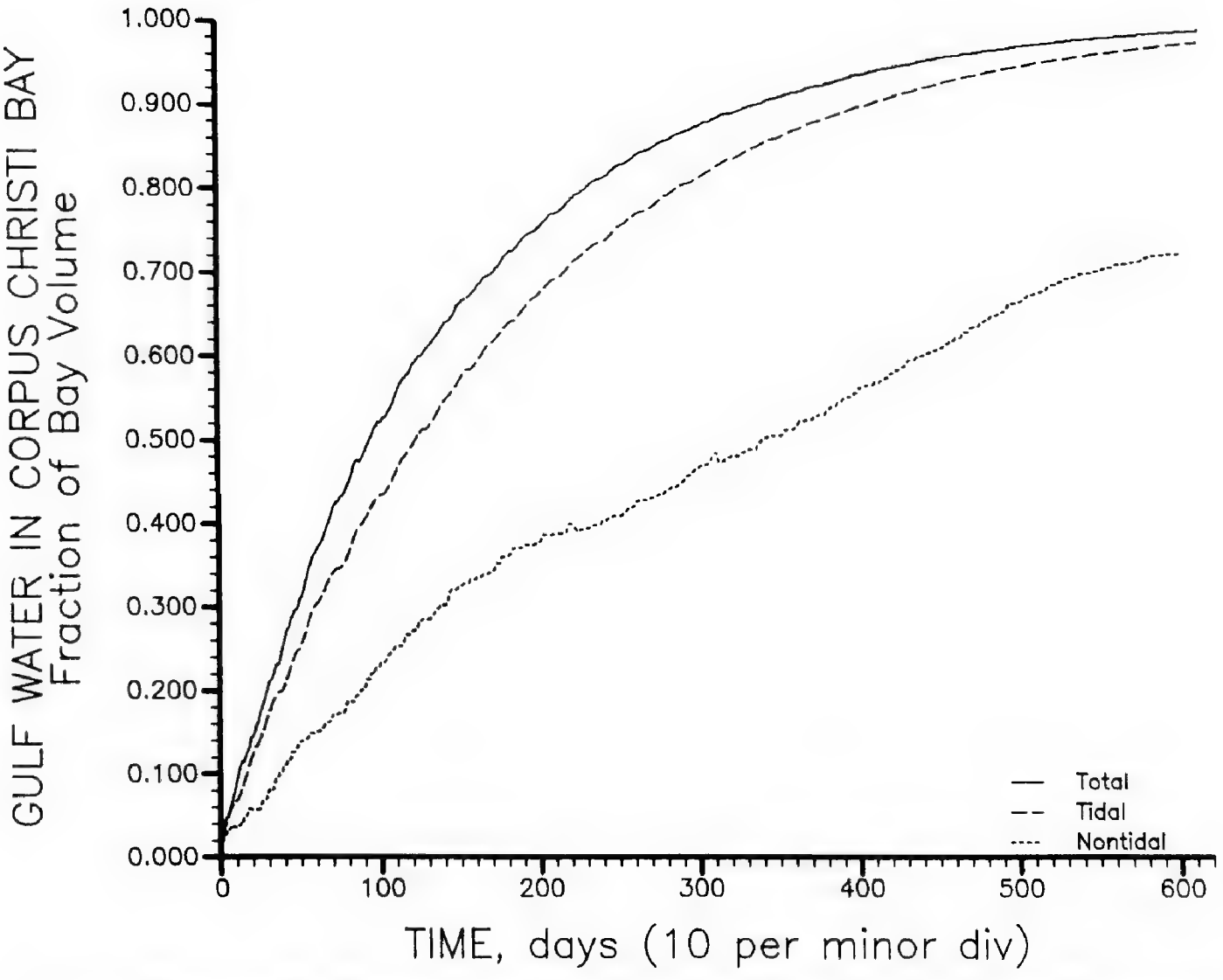

FIG. 4. Fraction of Gulf water accumulated in Corpus Christi Bay during the 610-day study period (13 November, 1973 through 15 July, 1975) in response to total (top curve), tidal (middle curve) and nontidal coastal water level variations (bottom curve).

calculations were made using the total water level variation recorded at the coast. The upper solid line traces the total net accumulation of Gulf water in Corpus Christi Bay. An initially rapid increase in the fraction of Gulf water is followed by a leveling off, as ebb tides begin to remove some of the Gulf water which has accumulated in the bay, and the curve asymptotically approaches 100%. For comparison purposes, it is noteworthy that the curve passes through the 0.5 level (50%) 105 days into the simulation. By the end of the 610-day study period, 97.8% of the water in the bay at the start of the calculations has been replaced by Gulf water.

The broken-line curves in Fig. 4 represent tidal and low-frequency flushing individually. Tidal exchanges were quantified by the model after the harmonic constants of the principal tidal constituents had been determined from a least squares harmonic analysis (Schureman 1941), and these values were used to create a time series of purely tidal water level variations (Pore and Cummings 1967). Subtidal frequency exchanges were isolated using a 40-hour low-pass numerical filter on the 610-day record of total water level variations. The degree of similarity between the total and tidal

flushing curves suggests that the tidal exchange comprises a substantial fraction of the total. For tidal processes alone, 50% of the water in the bay at the start of the simulation is replaced in the first 122 days. The half-life of bay water removed by low-frequency meteorological forcing is substantially longer. The first 50% of the bay water is not replaced until 339 days into the simulation, and by the end of the calculations only 72% of the bay water has been renewed by Gulf water.

Not pictured, but quantified by the model nonetheless, is the cumulative amount of Gulf water moving through Corpus Christi Bay and into each of the three adjacent bays on the landward side. This, in itself, does not represent a true flushing action for Corpus Christi Bay, because this water is only stored temporarily in these bays at times of generally rising water levels at the coast. When sea level falls, this water will re-enter Corpus Christi Bay from the landward side, forcing bay water out into the Gulf and completing the flushing action. The movement of Gulf water through Corpus Christi Bay forms the basis for quantifying the flushing of the inner bays. Model results indicate that the half-life values for Nueces Bay and Oso Bay are 148 days and 187 days, respectively. These inner bays are flushed with Gulf water more slowly, because Corpus Christi Bay must be charged with Gulf water first. The half-life of Laguna Madre was too long to be quantified with the available data. At the end of the 610-day simulation, only 9% of the volume of Laguna Madre had been replaced by Gulf water.

The question of the model's sensitivity to the assumed mixing rate is addressed in Fig. 5, which is a composite of three curves obtained using three different mixing rates. For simplicity, only the mixing rate of the Gulf water plume entering the eastern side of Corpus Christi Bay (see Fig. 1) has been altered in these calculations. It is noteworthy that all three curves have very nearly re-converged by the end of the 610-day study period. The maximum spread in the fraction of Gulf water in the bay occurs approximately 150 days into the simulation, when a 20% per hour mixing rate results in approximately 12% more Gulf water in the bay than occurs with a 10% per hour mixing rate. At the 50% renewal level, the 20% per hour mixing curve leads the 10% per hour curve by 31 days. A better estimate of the half-life of the bay—whether within or outside of this range—can be obtained only following a careful field study, using an appropriate tracer to distinguish between Gulf and bay water. Model results suggest, however, that unless the 15% per hour mixing rate value used here is well off the mark, the true half-life of bay water will not deviate from the 105-day value by more than a few weeks.

DISCUSSION

The +0.976 correlation coefficient for the simulated bay volumes and those calculated from water level recorders surrounding the bay lends considerable weight to the assumption that the barotropic pressure gradient, and the resulting two-way exchange process considered by the model, is of

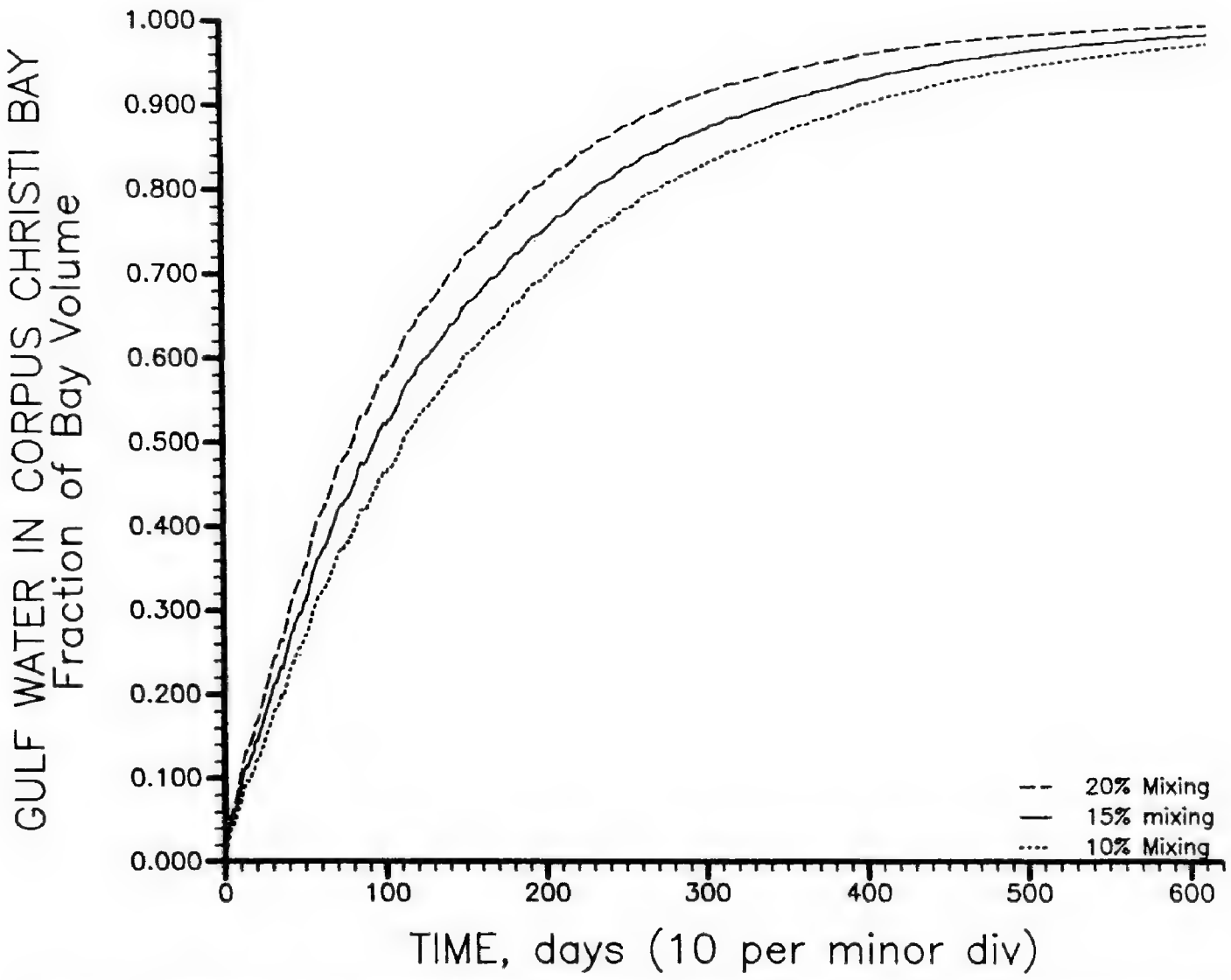

FIG. 5. Fraction of Gulf water accumulated in Corpus Christi Bay during the 610-day study period (13 November, 1973 through 15 July, 1975), assuming a 20% (top curve), 15% (middle curve) and 10% (bottom curve) per hour mixing of Gulf water entering Corpus Christi Bay.

primary importance in explaining the variance in the time series of Corpus Christi Bay volumes. Stream gage data were not examined for the 49-day calibration period (January–March, 1972), but it is likely that freshwater run-off was low at that time. Precipitation amounts are characteristically low in winter months. Substantial freshwater inflow could only reduce the correlation coefficient, because it would affect bay volumes to a greater extent than it would influence coastal water levels, and hence simulated bay volumes. At times of low run-off, then, the simple model described here appears to reproduce the two-way exchanges faithfully.

At times of high run-off, the simulated volumes would explain bay-shelf exchanges no less accurately, but one must then think of this process as occurring in concert with the movement of fresh water through the system. Although high run-off through the Texas coastal zone is the exception to the rule, it is appropriate to note that effects can be significant. For example, the U.S. Geological Survey stream flow data for the Nueces River indicate only three run-off events in 1974 involving discharges in excess of 30 m^3/s (the multi-annual mean value reported by Diener [1975] is 20.6 m^3/s). The largest, however, during the first three weeks of September (study days 259–

280), brought a total of 208.5 million m^3 of fresh water to the bays and reduced the mean salinity of Nueces Bay from 16.9 to 6.5 parts per thousand (Holland *et al.* 1975). The importance of isolated, major freshwater run-off events in flushing the bays and reducing the half-life values noted here should not be ignored, but they are outside the intended scope of this study, dealing with the two-way, inter-bay and bay-Gulf exchanges.

A satisfying result of the study was the confirmation of the assumption that only one water level recorder is required to drive the simulations. In the course of the analysis, it was noted that any of the water level recorders positioned around the bay (Fig. 1) could have been used to estimate the bay volume itself with somewhat greater accuracy than that obtained from model results based upon coastal water level records. With bay water level records used to estimate bay volumes, correlation coefficients varied from 0.972 to 0.995, and the standard errors of the estimates ranged form 3.13 to 7.81×10^6 m^3. This, by itself, suggests that one should concentrate one's efforts within the bay and take advantage of the less energetic wave climate. However, one learns less about water level variations at the coast with a recorder in the bay than one learns of water level variations in the bay with a recorder at the coast. Only the effects of bay-shelf exchanges are measured with instrumentation in the bay, and one must postulate what the driving force might be.

It should be emphasized that the half-life estimates listed in this paper are based upon mixing rates which are thought to be realistic, but which are unsupported by field measurements. Thus, any similarity between the 122-day half-life obtained in this study for tidal flushing alone and the value of 155 diurnal tidal cycles calculated in an earlier study (Smith 1982) is coincidental. Similarly, the 105-day half-life calculated from the total water level variation at the Aransas Pass is not necessarily support for, nor supported by the 0.46 year (168 days) residence time reported by Armstrong (1982) for Nueces estuary (including Corpus Christi Bay and Nueces Bay). Armstrong's approach was based upon bay and inner shelf salinity data, and thus remains the best estimate of a residence time. This study indicates the relative importance of tidal and nontidal exchanges, but only when mixing rates are determined can half-life values be established with confidence. Then, too, can seasonal variations in the residence time, or other deviations from the mean, be explored in detail.

ACKNOWLEDGMENTS

I would like to express my appreciation to Mr. Mark Schmalz, who programmed the one-dimensional model; to Dr. J. Chris Evans, who wrote the program for calculating bay volumes from bay water level records; and to Ms. Elizabeth Smith, for her help in plotting the time series of computed and simulated bay volumes. Four reviewers commented upon an earlier version of the manuscript, and the paper benefited substantially from their constructive criticism.

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WEATHERING OF IXTOC-I OIL UNDER NATURAL CONDITIONS IN TANKS: CHEMICAL CHARACTERISTICS

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ABSTRACT

Fresh Ixtoc-I oil was weathered under natural conditions in three simulated, natural settings: oil on seawater (257 days); oil on an exposed beach (170 days); and, oil on a subtidal beach (177 days). The experiments were done in fiberglass and concrete tanks. The course of weathering was followed by measurement of physical properties, compound class analysis (silica gel), capillary gas chromatography and stable carbon and sulfur isotope ratios.

Early weathering appeared to be dominated by the physical processes of evaporation and dissolution. Saturated and aromatic hydrocarbons of low molecular weight decreased. Chemical and biological weathering later increased the asphaltene and polar fractions. The del-carbon-13 values of the whole oil, asphaltenes, saturates, aromatics, and polar fractions remained remarkably constant during the course of the experiments. These data are consistent with analyses made for a large suite of weathered Ixtoc-I samples occurring in the natural environment.

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INTRODUCTION

The June 3, 1979 blowout of the Ixtoc-I well in the Bay of Campeche resulted in hastened activities to characterize the oil in an effort to evaluate what effect it would have when it reached the Texas coastal waters (Parker 1979).

Ixtoc-I "mousse", a material of 60–70% water in oil emulsion, arrived in Texas coastal waters in early August after a probable transport time of about 10 weeks. Most of the early studies performed in our laboratories, however, used the "*Point Baker* mousse", a sample collected by the United States

Coast Guard cutter "*Point Baker*" on July 28, 1979 at 22°50′ N latitude 96°26′ W longitude, approximately 200 miles SSE of Port Isabel, Texas. Subsequent comparisons of the *Point Baker* mousse with other Ixtoc-I samples, including those collected in Texas coastal waters, showed that there were some definite compositional differences which must have been due to differences in the amount of weathering of the materials (Scalan, Winters and Parker 1982).

The immediacy of the toxicity studies required that we use the material at hand, namely the *Point Baker* mousse. However, the observed inhomogeneities of the Ixtoc-I materials (Scalan *et al.*, 1982) demonstrated need to document changes in the chemical and physical nature of the Ixtoc-I mousse as a function of "weathering". It was apparent that the degree of alteration was a function of more than just the length of time of exposure of the mousse to the environment. Some samples reaching Texas coastal waters resembled more closely fresh mousse sampled near the source than they did the *Point Baker* samples.

Oil spilled or discharged into the marine environment begins a compositional change almost immediately. This compositional change, or weathering, depends upon physical properties of the environment such as temperature, wind velocity, sea state, solar radiance, etc. (Parker and Winters 1982). It may also depend upon chemical and biological parameters such as salinity, nutrient availability, types and populations of various microbiota and the composition of the oil itself.

Immediate compositional changes are primarily due to losses through volatility and solubility and thus are dependent mostly upon the composition of the original oil. Some crude oils, as is the case for Ixtoc-I oil, are emulsion formers. One result of forming an emulsion, or "mousse", is reduction in evaporative loss from the oil. Instead of spreading out in a "slick" with a high surface area to volume ratio, the water-in-oil emulsion tends to be thicker and more viscous resulting in a much lower area-to-volume ratio.

The expected result of mousse formation would be to slow down the natural weathering of the oil. There would be less evaporation and solubilization. Because of reduced water-oil contact area, there would be less biological degradation expected. With less area exposed to the sun and air, a reduced rate of photo-oxidation would also be expected.

Some studies have been reported concerning observed variations in chemical composition of Ixtoc-I oil. Lee, Morris and Boatwright (1980) reported a lack of acute toxicity was related to compositional changes due to apparent weathering. Mackay, Paterson, Boehm and Fiest (1981) formulated a mathematical model for weathering of Ixtoc-I oil based on compositional variations of mousse, and related water column samples. Both of these studies used samples collected from the natural environment for which the past history was known only by speculation. Overton, Lasater, Mascarella, Roschke, Nuiry and Farrington (1980) show the effects of photo-chemical oxidation of Ixtoc-I oil which had been collected at the well site and presumably had little exposure to natural weathering. Botello and Castro-

Gessner (1980) show chemical and isotopic changes in a synoptic suite of samples taken 47 to 51 days after the spill began.

Estimates of the quantity of oil released into the marine environment by the Ixtoc-I blow-out vary widely but 3.3×10^6 barrels is a consensus value (Gundlach, Finkelstein and Sadd 1981). Of that amount, some 7.8×10^4 barrels probably reached Texas coastal waters (Gundlach *et al.* 1981). In populated areas and those readily accessible the oil was reasonably-well cleaned up. While in isolated areas there was no attempt to remove the beached oil, measures were taken to keep the oil from impacting the more sensitive bays and estuaries.

A great amount of oil remained on the shore and in the near shore sediments (Rabalais and Flint 1982; Amos, Rabalais and Scalan 1983). It is important to be able to recognize this material in the future and to predict what physical and chemical changes might be expected from weathering and biological alteration. The following experiments were undertaken to help expand our knowledge of the long term effects of weather on spills.

EXPERIMENTAL

SAMPLES

The starting material for these experiments was relatively fresh material collected at the well-site by Oil-Mop Inc. The material was not a mousse and still contained approximately two percent of low boiling point material (molecular weight less than 150). No analysis was made to detect the presence of additives such as emulsion-breakers in this material, however, the oil readily formed a stable "mousse", therefore it is not believed that such materials were present.

A fresh mousse was prepared at the start of each experiment by addition of oil to a calculated amount of seawater to yield a water-in-oil emulsion of approximately seventy percent water by weight. The mixture was thoroughly blended in a Waring Blender to give a mousse that was essentially indistinguishable from fresh mousse collected from the Gulf of Mexico.

In some experiments an "aged" mousse was used. For these studies the freshly prepared mousse was exposed to natural heat and sunlight on the roof of the laboratory building for a period of two weeks before use. In the beach and subtidal exposure experiments some fresh unemulsified oil was used in addition to "mousse".

SPILL ENVIRONMENTS

Controlled mousse spills were conducted in three simulated sites:

(1) A tank of sea water 3m in diameter and 1m deep was used to simulate the open-ocean environment. The tank was constructed of fiberglass and was equipped with a circulating water system. The circulating water was discharged around the periphery of the tank in a water cascade to keep floating mousse away from the edge of the tank. A simple wind baffle kept strong, northerly winter winds from disrupting the water-cascade containment system.

Two water column spill experiments were conducted. One was a winter spill starting on 12 January 1981, lasting 257 days until 25 September 1981. The other water column spill started 13 May 1981 and lasted until 135 days later on 25 September 1981. In both cases the material spilled was a freshly prepared mousse sample.

(2) Subtidal spill experiments were simulated by sediments contained in an almost circular concrete tank 4.3 m in diameter and 0.6 m deep. Twenty centimeters thickness of fine-grained

beach sand was covered with thirty-five cm of sea water. Spills occurred before the sea water was added. Fresh and "aged" mousse were ladled on to the sediments and in some cases were buried beneath 0.5 to 3 cm of sediments. Seawater was drained from the tank to permit sampling. The experiment began on 27 April 1981 and continued for 177 days.

(3) A beach-foredune environment was prepared in a concrete tank similar to that described above. Beach sands were maintained at three elevations in the tank by means of concrete blocks. Seawater was passed through the lowest level of the tank where the elevation of beach sand was not more than 10 cm above the seawater. The intermediate elevation contained sand 15–25 cm above the seawater. Sand in the highest level was 30–45 cm above the running seawater. Fresh or aged mousse was poured onto or mixed into surface sand at each of the three elevations. Fresh or aged oil was also buried 2–3 cm beneath the sand at each elevation. The experiment was begun May 5, 1981 and terminated 170 days later.

CHEMICAL ANALYSES

The first step in the analytical procedure was removal of extraneous sand or seawater from the oil to be examined. An equal volume of hexane was added to approximately 25 ml mousse samples taken from the seawater tanks. The mixture was centrifuged at 12,000 RPM for 15 minutes. The asphaltene-free oil dissolved in hexane was removed from the centrifuge tubes by pipet. Asphaltenes which precipitated from the oil were collected by filtering the remaining contents of the centrifuge tube through a glass fiber filter. Samples from the subtidal or beach tanks were dissolved in an equal volume of benzene and allowed to settle for at least one hour. The oil in benzene was decanted away from sand and water which settled to the bottom and sides of the container. A small amount of fresh benzene was added to the residue and the remaining oil was removed by pipet. Benzene was removed from the samples by careful evaporation with nitrogen gas at 40 to 50°C. Asphaltenes were then precipitated and removed after addition of 4–5 volumes of hexane.

About 500 mg of asphaltene-free oil was chromatographed on a 2.2 × 24 cm column of silica gel (ICN Pharmaceuticals activity I). Three fractions were eluted: a saturated hydrocarbon fraction was eluted with two column volumes of hexane; an aromatic fraction eluted with an equal volume of a hexane:benzene (1:1) mixture, and a polar fraction eluted with a volume of methanol sufficient to elute all color. Saturate and aromatic fractions from each sample were carefully evaporated to 10 ml under nitrogen gas at 40 to 45°C. A 1 ml portion of saturate and aromatic fractions was then removed and set aside for gas chromatographic analyses.

The remainder of the saturate and aromatic fractions were transferred to a weighed vial and evaporated as before to about 1 ml. Fractions were then covered by an inverted beaker and allowed to evaporate at room temperature. Polar fractions were evaporated to dryness, transferred to a weighed container with chloroform and evaporated to constant weight.

Gas chromatography was carried out on a Perkin-Elmer 910 gas chromatograph equipped with a flame ionization detector. Electronic integration of peak area was performed by a Hewlett-Packard 3352B Data System. The fused silica column utilized for analyses was OV-101, 25 m. Oven temperature was programed from 70 to 265°C at 4°/min and held at 265°C for 35 minutes.

Stable carbon and sulfur isotope analyses were performed on many of the whole oils and their separated fractions and are reported as $\delta^{13}C$ and $\delta^{34}S$. The method of determining $\delta^{13}C$ and $\delta^{34}S$ are described in the literature (Calder and Parker 1968) and will only be summarized. Organic matter is converted to CO_2 for carbon mass analysis by a method modified from Sofer (1980). Sulfur isotopes, $\delta^{34}S$, were measured on SO_2 which was prepared by a sealed tube method modified from that of Holt and Engelkemeir (1970) and Bailey and Smith (1972).

The mass spectrometer used for isotope analysis was a VG-Micromass model 602E, 90° sector field, double collector instrument. The isotope analyses are expressed in terms of the parts per thousand (per mil) difference between the isotope ratio of sample and that of an arbitrary standard

$$\delta^{13}C = \frac{(^{13}C/^{12}C)\ \text{sample} - (^{13}C/^{12}C)\ \text{std.}}{(^{13}C/^{12}C)\ \text{std.}} \times 10^{3}‰$$

An analogous expression is used for the ^{34}S definition. The standard for carbon is the Peedee belemnite (PDB) carbonate; $\delta^{34}S$ variations are reported relative to the Canyon Diablo meteorite. The experimental errors for measurement for sulfur and carbon analyses are better than ± 0.5 and ± 0.2% respectively.

RESULTS AND DISCUSSION

STABLE ISOTOPE RATIO VARIATIONS

A major goal of this project was to determine the changes which stable carbon and sulfur isotope ratios of Ixtoc-I oil and its components undergo during known weathering conditions. These ratios which have long been used in the petroleum industry for exploration, are being considered for level one indicators or tracers for specifc oil spills. Both the NOAA RESEARCHER/PIERCE IXTOC-I Cruise and the BLM/ERCO study had sub-projects by several chemists designed to measure stable isotope ratios on a large suite of samples taken from the environment at locations where Ixtoc-I oil was expected (Sweeney, Haddad and Kaplan 1980; Botello and Castro-Gessner 1980; Mankiewicz and Kaplan 1982).

A. Oil on Water

The $\delta^{13}C$ values of Ixtoc-I oil and oil fractions are summarized in Table 1.

TABLE 1

$\delta\ ^{13}C_{PDB}$ (‰) of Ixtoc-I oil during weathering: oil on water.

Sample	Whole Oil	ASPH	SAT	AROM	NSO
New Mousse					
January 1981					
Day 0	-27.4	-27.2	-27.7	-27.2	-26.9
Day 1 to 6	-27.2	-27.3	-27.3	-26.9	-26.6
	±0.15	±0.08	±0.07	±0.11	±0.12
Day 8 to 14	-27.2	-27.5	-27.5	-26.8	-26.7
	±0.13	±0.21	±0.2	±0.15	±0.07
Day 18 to 43	-27.2	-27.4	-27.4	-27.3	-26.8
	±0.16	±0.29	±0.07	±0.36	±0.1
Day 50 to 95	-27.0	-27.4	-27.4	-27.3	-26.6

ASPH Asphaltenes
SAT Saturate hydrocarbons
AROM Aromatic hydrocarbons
NSO Polar fraction

The $\delta^{13}C$ value of the whole oil varied less than 0.2 per mil during the first 43 days and by only 0.4 per mil to day 95. Since these data represent many measurements, one can be fairly confident of the limited variation. The $\delta^{13}C$ values for the saturate fraction varied by 0.4 per mil during the 95 day

period. The aromatic fractions became 0.5 per mil more negative during the first 14 days then returned to within 0.1 per mil of the day zero value during the last 77 days of the experiment. This behavior is small but probably real. It is remarkable that the NSO fraction varied only 0.3 per mil over the 95 day period. One would have expected this fraction to be the most chemically reactive material. The asphaltic fraction showed a change of only 0.3 per mil during the course of the experiment.

In summary, the $\delta^{13}C$ values of the whole oil, asphaltenes, saturate fraction, aromatic fraction, and the NSO fraction were remarkably constant during the 95 day experiment. Variations that were observed were close to the ± 0.2 per mil resolution which is possible with routine sample analysis. While the whole oil and fractions all seemed well behaved with respect to isotopic changes with weathering, it is clear that any study would be strengthened by measuring several parameters rather than just this one.

Measurements made of $\delta^{34}S$ during the course of the pond weathering experiment gave the following data:

Day 0 −5.1
Day 155 −4.1
Day 170 −3.8.

This trend toward more $\delta^{34}S$ enriched material is consistent with a study of eight Texas (Ixtoc-I derived) beach tars, −4.2 which we reported earlier (Scalan *et al.* 1982). It is also consistent with sulfur data reported in the NOAA and ERCO/BLM study (Sweeney *et al.* 1980). except that not as wide a range was seen in the pond weathering study. While more work is needed to establish the validity of the method, a measurement of sulfur isotope composition may reflect the relative weathering of the oil samples.

B. Artificial Beach Experiment

The isotope data for the artificial beach study again demonstrated that $\delta^{13}C$ is remarkably constant during weathering. Whether the mousse was buried in sand or left exposed on the sand surface did not strongly influence the data (Table 2). Results obtained in this study are consistent with carbon

TABLE 2

$\delta\ ^{13}C_{PDB}$ (‰) of Ixtoc-I oil during weathering: oil on beach.

Oil type/ Location	Whole Oil	ASPH	SAT	AROM	NSO
Fresh mousse Day - 0	-27.4	-27.2	-27.7	-27.2	-26.9
Fresh mousse/ Buried in sand	-27.8 (1)	-26.9 (1)	-27.9 ±0.1	-27.4 ±0.2	-27.5 ±0.3
Fresh mousse/ on sand	-27.5 ±0.3	-27.2 ±0.2	-27.8 ±0.3	-27.4 ±0.3	-27.6 ±0.2
Aged mousse/ on sand	-27.4 (1)	-26.9 (1)	-27.7 ±0.4	-27.1 ±0.4	-27.3 ±0.1

All data is the average of days 66, 107, 155 and 170.

isotope values obtained for a large suite of tarballs collected from Mexican beaches during the fall of 1979 (Table 3). The carbon isotope data of Table 3 strongly suggests that oil on ten of the eleven beaches sampled was Ixtoc-I oil. The isotopic profile of the La Pesca sample was different from the Ixtoc-I samples.

TABLE 3

$\delta\ ^{13}C_{PDB}$ (‰) of tarballs collected from Mexican beaches in the fall of 1979.

Sample Location	Saturate	Aromatic	NSO
Matamoros	-27.8	-26.9	-26.7
La Pesca	-25.9	-24.8	-25.1
Tampico	-27.1	-26.8	-26.7
Tuxpan	-27.4	-27.4	-27.1
Veracruz	-27.3	-27.0	-26.9
Alvarada	-27.3	-26.8	-26.8
Coatzacoalcos	-27.1	-26.9	-26.7
Barra Tupilco	-27.4	-	-26.9
Isla del Carmen	-27.4	-27.0	-26.7
Celestum	-27.9	-26.9	-26.7
Santa Clara	-	-26.8	-26.9

Stable isotope data appears to provide a parameter which permits identification of oil which has been weathered to such an extent that many parameters of identification are useless.

CHEMICAL STUDIES

A. Oil on Water

Chemical changes were most readily observed in the tank experiments. One of the most striking changes was in the asphaltene content of the mousse. Figure 1 shows a plot of asphaltene content of mousse versus time for the tank experiment. Although the experiment included another sampling at 257 days the asphaltenes content could not be measured according to our standard techniques since the whole material was no longer a mousse but rather a flakey semi-solid.

Another, perhaps related, change can be seen in the relative quantities of polar compounds not precipitated as asphaltene. This relationship as a function of time is shown in Fig. 2. There are possible contributions of volatility and dissolution to this change but they are considered negligible. There is an apparent anomalous value at day 127 showing a degree of weathering more comparable to only a few tens of days. This anomaly is discussed later.

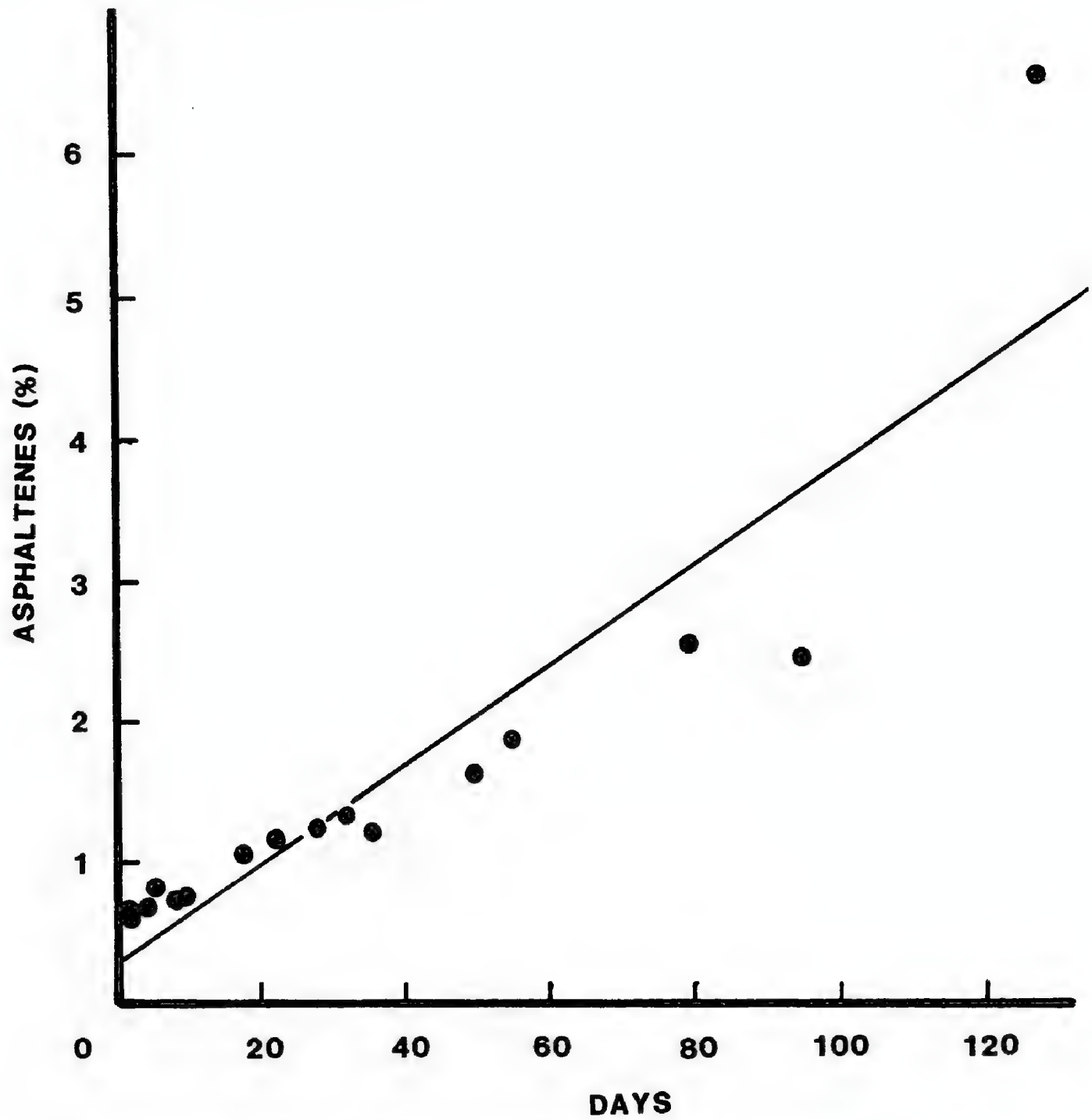

FIG. 1. Asphaltenes content of Ixtoc-I mousse samples floating on seawater.

A measure of the possible loss of material through volatility might be found in the distribution of the saturated hydrocarbons. Representative chromatograms are given in Fig. 3. In general there is a preferential loss of the lower molecular weight hydrocarbons with a concommitant increase in the carbon number of the most dominant n-alkane.

Again, the sample at day 127 is anomalous. The lower molecular weight compounds have not disappeared as readily as some earlier samples and the most dominant alkane is more like that of a sample aged only a few weeks. This is more readily observed in Fig. 4. This figure shows a plot of the carbon number of the alkane of highest relative concentration versus time in days for the tank experiment.

Table 4 shows various ratio parameters for the oil on water experiment. The isoprenoid compounds pristane and phytane are somewhat uniform in

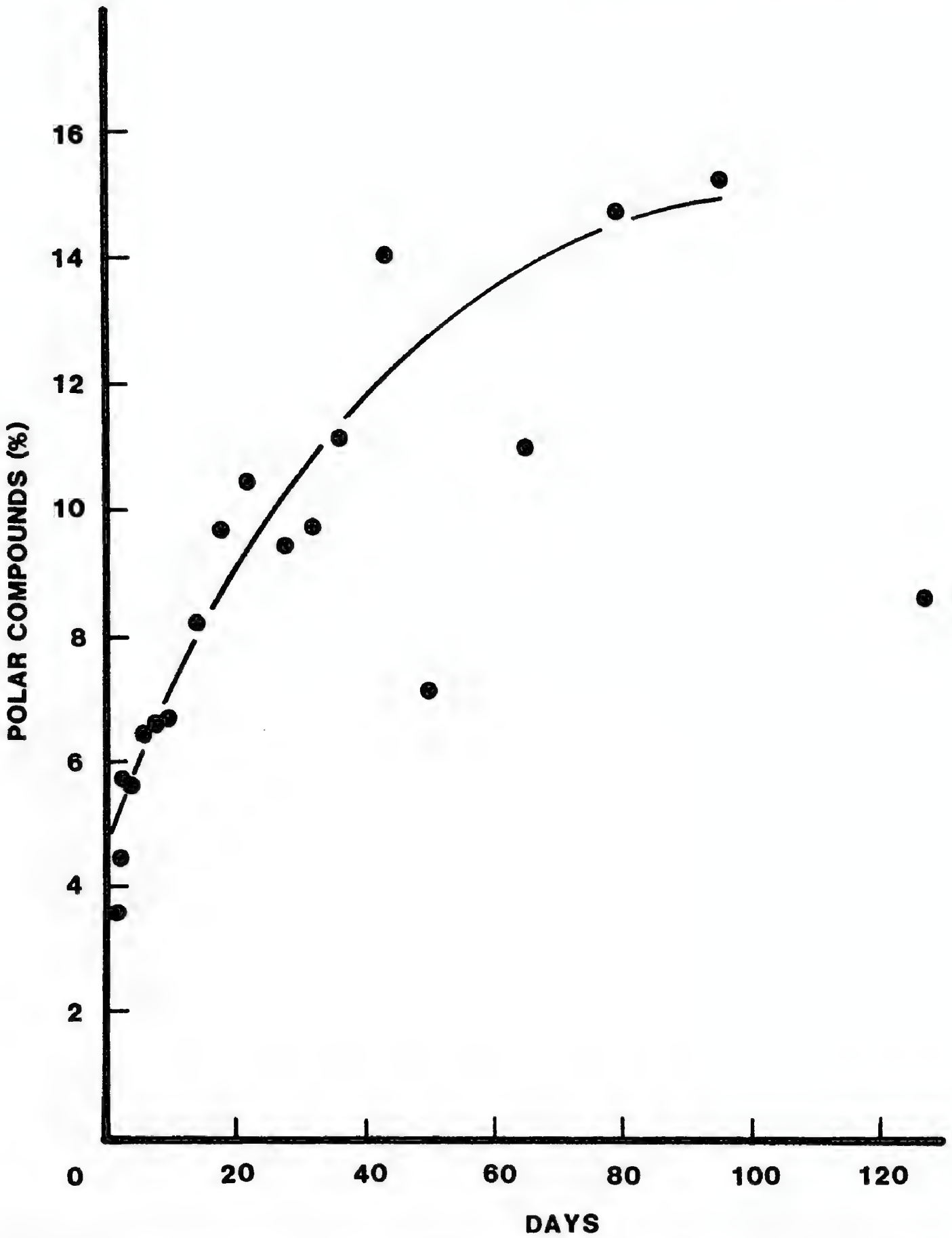

FIG. 2. Relative percentage of polar compounds separated from weathered Ixtoc-I oil floating on seawater.

their relative ratio. The ratio of the sum of n-alkanes 17 and 18 to the sum of the isoprenoids pristane and phytane is also relatively insensitive to the degree of weathering. Only the sample at day 257 shows a departure from this measure. This is interpreted as an indication of considerable biodegradation in this sample.

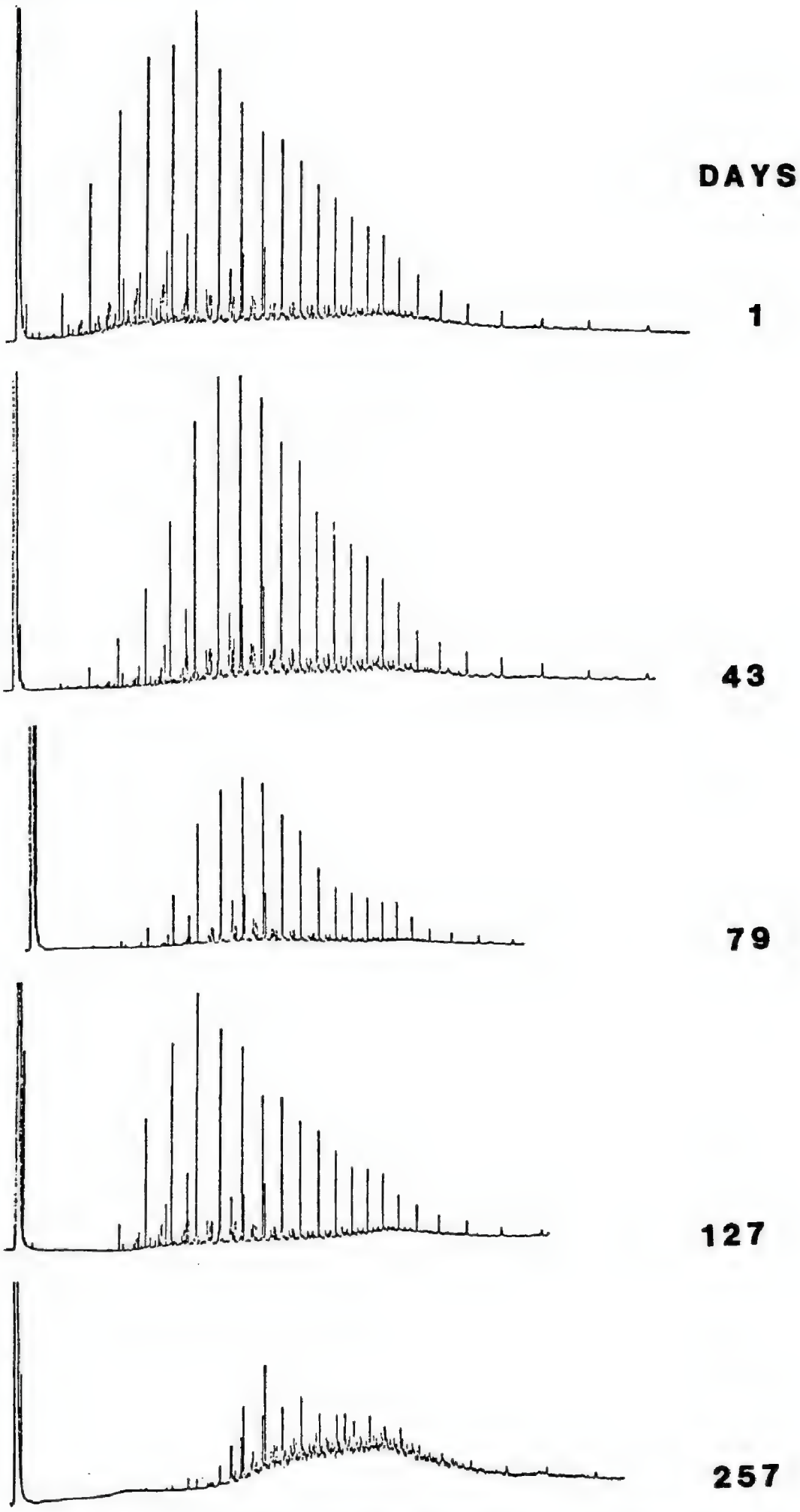

FIG. 3. Representative chromatograms of saturated hydrocarbons separated from weathered Ixtoc-I oil floating on seawater.

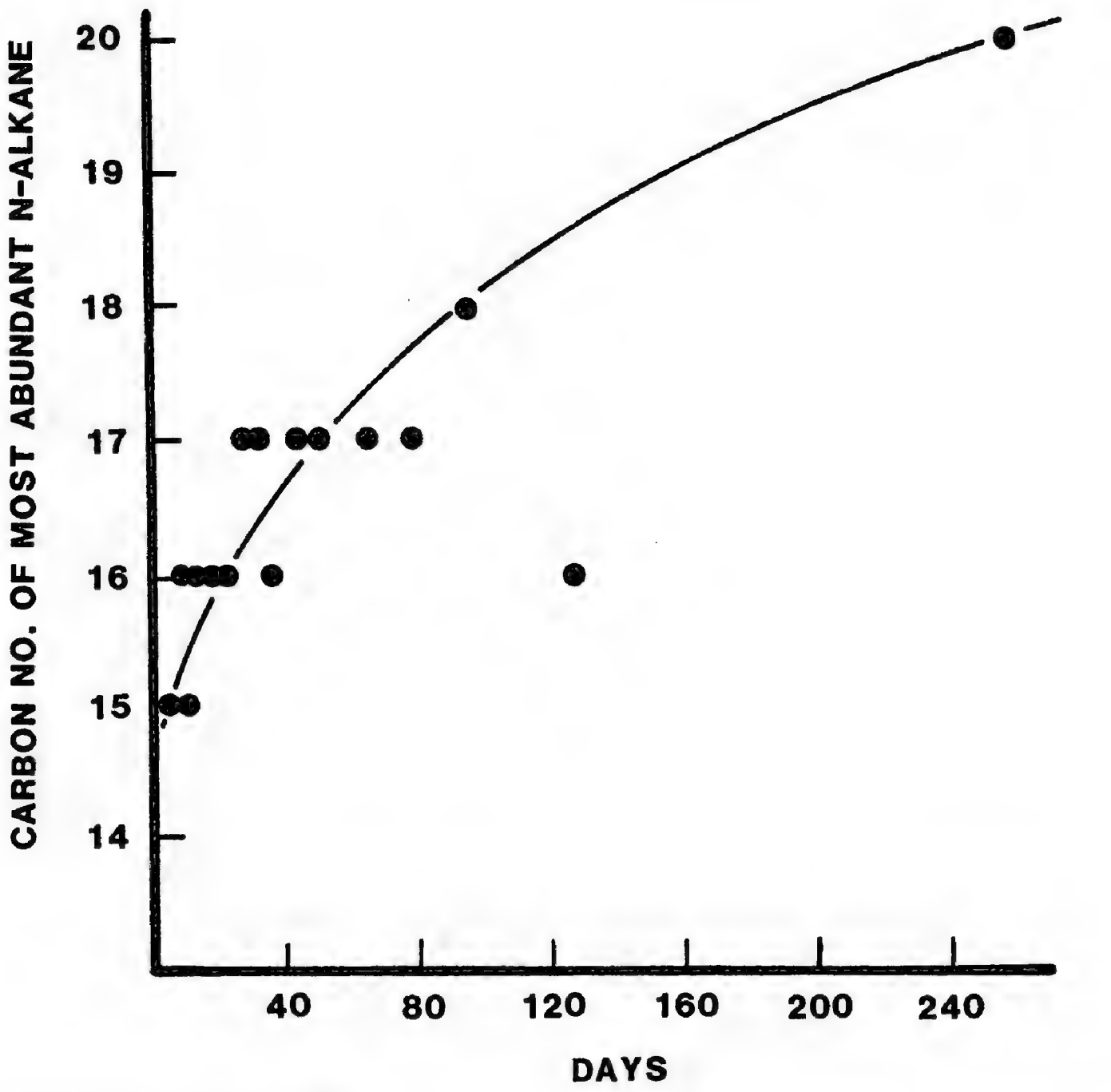

FIG. 4. Distribution of most abundant n-alkane of saturated hydrocarbons separated from weathered Ixtoc-I oil floating on seawater.

TABLE 4

Ratio parameters of Ixtoc-I oil during weathering: oil on water.

Sample	n-C17/n-C18	ip16/ip18	ip18/pris	pris/phyt	(n-C17+n-C18)/(pris+phyt)
Day 1 to 6	1.10 ±.03	0.87 ±.04	1.15 ±.10	0.91 ±.08	2.43 ±.12
Day 8 to 14	1.18 ±.03	1.10 ±.26	0.93 ±.21	0.94 ±.02	2.43 ±.07
Day 18 to 43	1.14 ±.06	0.87 ±.21	0.79 ±.16	1.00 ±.20	2.11 ±.19
Day 50 to 95	1.09 ±.05	0.70 ±.12	0.67 ±.03	0.96 ±.09	2.14 ±.06
Day 257	0.74	---	0.66	0.59	0.48

Figure 5 shows a portion of the infra-red spectra in the region of 5 to 7

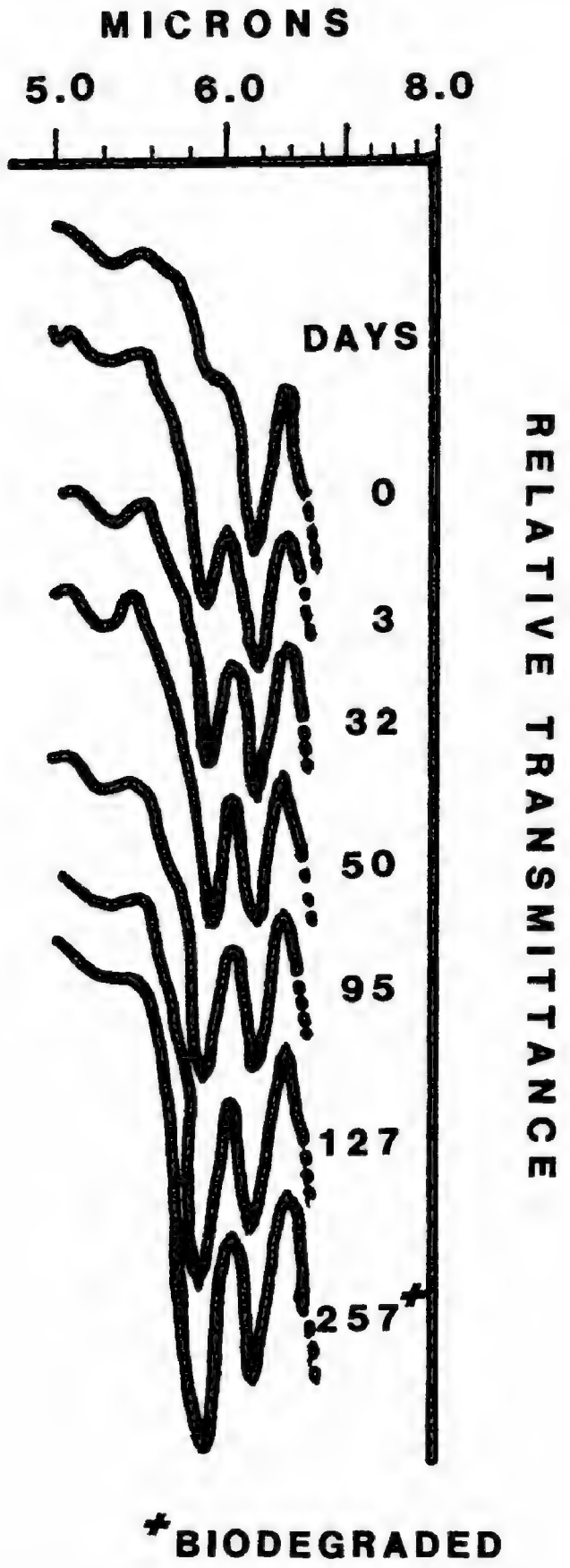

FIG. 5. Infrared absorption of weathered Ixtoc-I mousse floating at the seawater surface.

nanometers. The peak at 5.85 nm is due to carbonyl stretching in acids and esters while that at 6.2 to 6.4 is most likely due to aromatic carbon-carbon bonds. In this case the day 127 sample does not appear to be anomalous. The carbonyl compounds are most likely a result of photo-oxidative processes.

Aromatic components show the same sort of relationship as the alkanes. In Fig. 6 is seen a loss of the lower molecular weight aromatics with time.

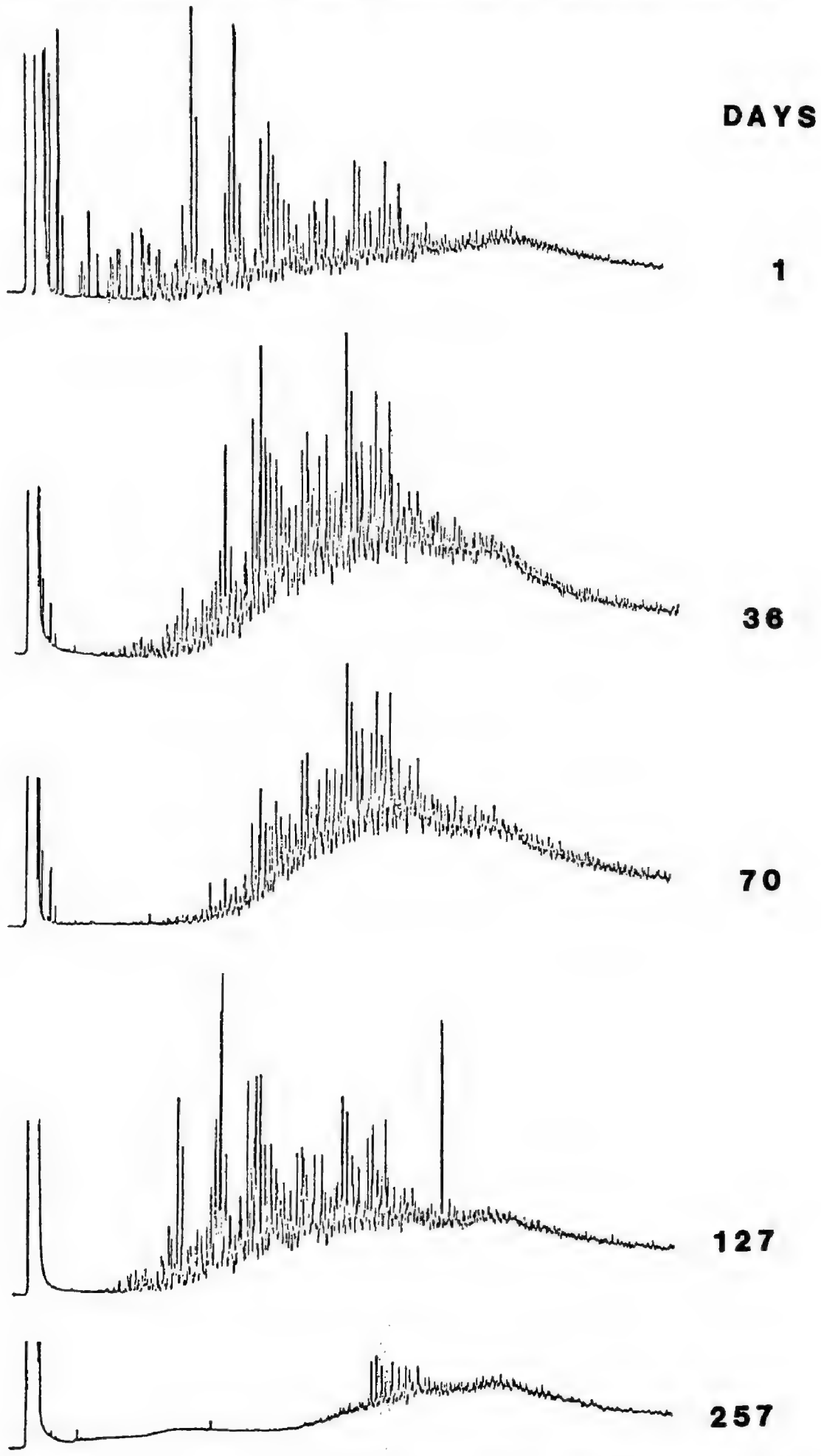

FIG. 6. Distributions of aromatic hydrocarbons in weathered Ixtoc-I mousse floating at the seawater surface.

The components which seem to persist even in the highly weathered and biodegraded sample of day 257 are substituted dibenzthiophenes. Notice that once again the sample at day 127 does not fit the general pattern. Mono- and di-methyl substituted naphthalenes still dominate the chromatographic record. (The one lone peak at higher molecular weight is believed to be a phthalate contaminant).

The degree of weathering of a sample depends upon the degree of exposure to the environment. In the case of the mousse on the surface of seawater, the initial exposure was a continuous, thick surface exposed to the water on one side and the sunlight and elements on the other. As weathering progressed the continuous sheet broke up into smaller "pancake" like portions ten to twenty centimeters diameter. With still more weathering the floating portions become more consistent and smaller, averaging 5 to 10 cm across. These small "cakes" were overturned periodically so as to expose the underside and provide uniform weathering. Some portions were of such a dynamic shape that they were stable with only one side upward. This property may have served to protect these particles from extensive weathering. This is believed to be the case for the sample taken on day 127.

B. Artificial Beach Experiment

The impingement of the oil on the beach provided a different environment for various weathering processes. In general the petroleum is protected from sunlight and air oxidation when buried beneath the sand or submerged beneath the water. Weathering alterations are reduced or slowed down. On the other hand the emulsion is mostly broken down and the protection afforded by the mousse is no longer effective. Where the beach environment is exposed and dry such as in a dune or foredune area, degradation proceeds for that material exposed. Where the sands are wet, there is a greater opportunity for biodegradation of the oil.

These generalizations were observed in the simulated environment. Infrared spectra of "mousse" spilled on the simulated beach environment are shown in Fig. 7. The growth of the carbonyl containing compounds in the whole oil is again evident. The sample on day 170 shows less photo-oxidation than the other samples. This sample was recovered from dry sand of a simulated foredune area whereas the other samples were from the "littoral" zone (wet sands) of the simulated beach.

Protection from sunlight retards the weathering process considerably. Figure 8 shows the infrared spectrum of a sample of mousse weathered for 177 days. In this case, the sample site was a simulated subtidal oil reef. The mousse was mixed with sand and submerged beneath 35 cm seawater. Even after 177 days the degree of weathering is comparable to that of only a few weeks for exposed material in the tank experiments.

SUMMARY

Some of the more significant observations of this study are:

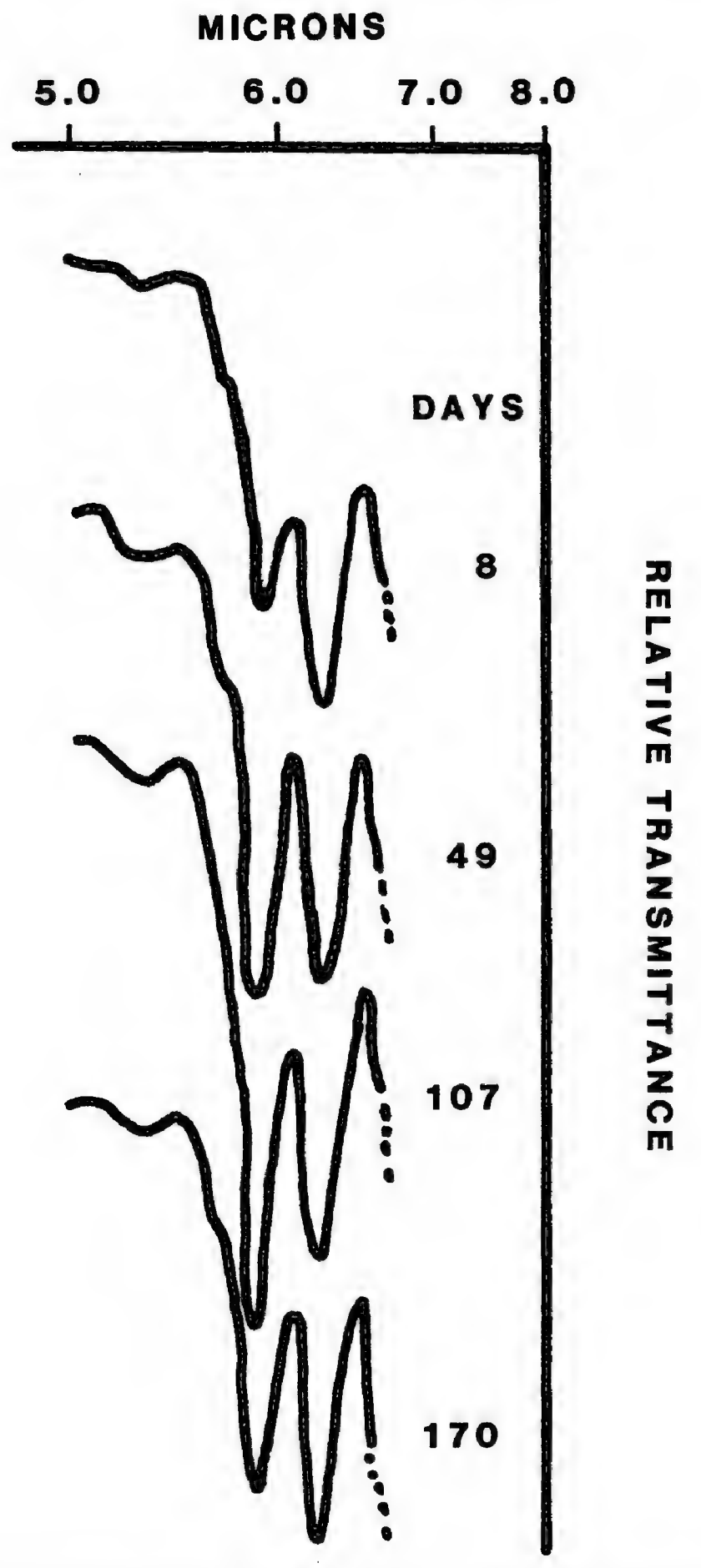

FIG. 7. Infrared absorption of weathered Ixtoc-I mousse on the sand of a simulated beach.

(1) Stable carbon and sulfur isotope ratios are useful parameters for identification of crude oils, even when they are highly weathered.

FIG. 8. Infrared absorption of Ixtoc-I mousse weathered 177 days in a subtidal pool.

(2) Exposure to sunlight, evaporation and oxidation appear to have been the most important factors in determining the extent of weathering during the first three or four months.
(3) Large differences in the rate of weathering may exist among subsamples of a given oil with similar environmental histories at the air/water interface due to particle shape. Possibly this is an artifact of the relatively calm surface of the experimental tanks. The importance of this process in the world's oceans remains untested.

ACKNOWLEDGMENTS

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BENTHOS STRUCTURE AND FUNCTION IN A SOUTH TEXAS ESTUARY[1,2]

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ABSTRACT

The Corpus Christi Bay estuary in the northwestern Gulf of Mexico was investigated for spatial and temporal variation of benthos community structure and function. Four stations were sampled quarterly for 2.5 years to investigate for macroinfaunal species assemblage changes as well as changes in benthic metabolism and nutrient regeneration. Cluster analysis of species assemblages illustrated that community structure changed from the riverine-influenced end of the estuary to the oceanic-influenced end. Taxa number increased away from the fluvial source while total abundance decreased. Maximum biomass was observed in the middle estuary region. Although spatial patterns were evident, no consistent seasonal patterns were observed for community structure characteristics from one site to the next. Community functional processes were not significantly different between sites. Metabolism did not show consistent temporal patterns but sediment nutrient flux always exhibited peak rates during the summer at all sites.

Sediment texture differences as well as variability in salinity between sites were thought to influence benthos structure and function in this estuary. Multivariate discriminant analysis differentiated communities according to (1) those that inhabited a less variable environment (salinity) and supported more benthic taxa, and (2) those that inhabited a significantly different kind of sediment, supported fewer taxa, and exhibited much greater faunal biomass with corresponding larger metabolic rates. A comparison with other estuaries indicated that Corpus Christi Bay benthic metabolic rates were intermediate and that nutrient regeneration rates were high in those estuaries where similar data were available.

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INTRODUCTION

The importance of benthic communities to estuarine-coastal ecosystems is illustrated by their well-defined role in the support of higher trophic levels (*e.g.*, Bell and Coull 1978; Arntz 1980; Poxton, Eleftheriou and McIntyre

1982). Evaluating the relationship between estuarine benthos and fisheries requires data on community structure and biomass. Information on the production of carbon and the role of the benthos in nutrient recycling however, are also required to define specific links between the benthos and other system components not normally derived from community structure descriptions alone. For example, associations have been established between estuarine benthic communities and biogeochemical cycling mechanisms in the sediments (*e.g.*, Rhoads, Aller and Goldhaber 1977; Aller 1978; Nixon, Kelly, Furnas, Oviatt and Hale 1980; Rhoads and Boyer 1982) suggesting an important link to ecosystem function in support of the food chain base (phytoplankton).

Estuaries of the mid-Atlantic and southeast United States, which are associated with productive coastal fisheries, have been described extensively; with respect to lower trophic levels and general ecosystem processes that provide the underlying support for these fisheries. Benthic communities have been characterized (*e.g.*, Bloom, Simon and Hunter 1972; Boesch, Diaz and Virnstein 1976; Young and Young 1977; Chester, Ferguson and Thayer 1983) and processes associated with the benthos, such as carbon production and nutrient recycling, have been quantified (*e.g.*, Nichols 1977, Aller 1980, Nixon 1981, Hopkinson and Wetzel 1982). Although northwestern Gulf of Mexico coastal waters support more than 15% of the annual U.S. fishery yield and 20% of its annual value (Flint 1984), characterization of lower trophic levels and processes supporting these fisheries are limited.

The Corpus Christi Bay estuary, one of seven major estuaries along the Texas coast, has been investigated over the last 10 years for benthic macroinfaunal community structure (Flint and Younk 1983). Although numerous temporal changes in community structure have been correlated with climatological events (Flint 1983), a major short-coming of these studies has been the inability to identify: (1) specific environmental characteristics that are related to the observed community structural changes within specific habitats, and (2) importance of these benthic communities to the rest of the estuary with respect to processes affecting ecosystem function. Therefore, the objective of the investigation described below was to evaluate spatial and temporal variation in benthic community structure and function simultaneously in different habitats of the Corpus Christi Bay estuary.

METHODS

A total of 10 stations were sampled in the Corpus Christi Bay estuary from July 1981 to October 1983. Four of these sites, stations 2, 7, 9, and 10 (Fig. 1) were chosen to measure benthic community variables because of their differences in habitat environment within the estuary. Station 2 was strongly influenced by fluvial flow to the estuary, stations 7 and 9 were considered mid-estuary sites with different sediment characteristics, and station 10 was approximately 8 km seaward of the barrier island beach and more ocean-influenced than the others. All 10 stations, including the four benthos sites, had water column variables and phytoplankton productivity measured, as described elsewhere (Flint 1984).

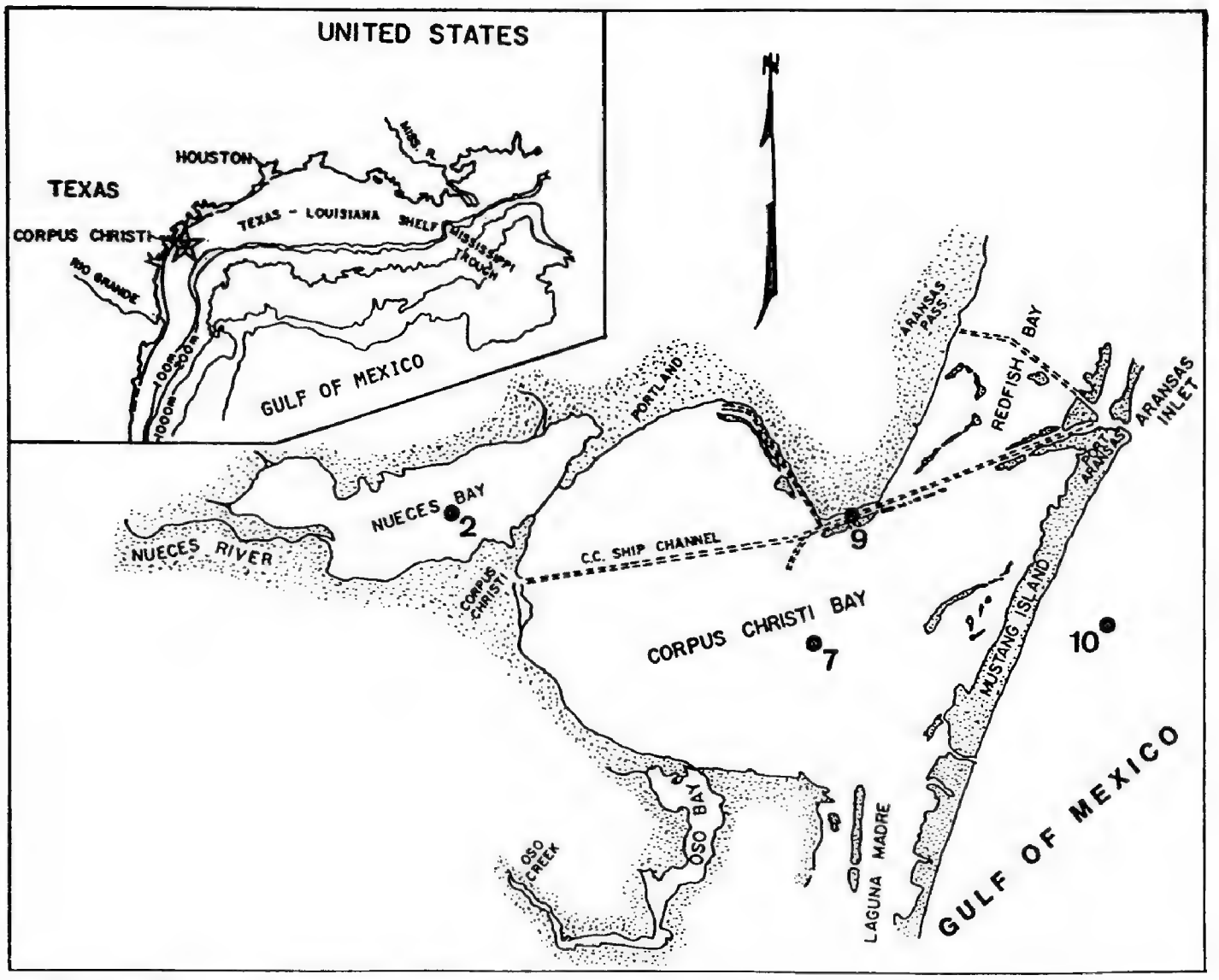


FIG. 1. Map of the Corpus Christi Bay estuary study area illustrating the benthic sampling sites investigated.

The benthos stations were sampled every 3 months (quarterly) during the 2.5 year study. Sediment sampling was accomplished using SCUBA. During each collection interval triplicate 7.5 cm diameter cores 30 cm long were taken simultaneously. These cores were capped and brought on-board ship. After sediment stabilization each core had Eh measured at 10 mm intervals using a Radiometer pH/Eh Meter with a platinum/calomel electrode system which was standardized against a reference Zobell solution (Whitfield 1979). Eh measurements were made to determine depth of the sediment redox potential discontinuity (RPD) layer, where the millivolt reading equals zero, as described by Rhoads and Boyer (1982). It is believed that the RPD indicates the deepest extent of oxygenated sediments and is thought to be influenced by infaunal bioturbation (McCall 1977; Rhoads, McCall and Yingst 1978).

The walls of each core tube were split to aid in sectioning the sediments. Cores were sectioned vertically 0–3 cm, 3–10 cm, and 10–20 cm. After core splitting, each sediment section was placed in 1 L jars and preserved with 10% seawater formalin containing Rose Bengal as a vital stain (Flint and Holland 1980). In the laboratory each section was sieved (0.5 mm mesh) and the retained benthic fauna identified and counted. Wet weight biomass was measured individually on the macroinfaunal species that dominated each station's sediments and on the entire faunal sample.

Additional sediment cores at each station were obtained by diver during each sampling interval for sediment surface (0–6 cm) water content, grain size analysis, and determination of organic carbon. Sediment texture parameters were determined (Flint and Younk 1983) and percent total organic carbon was measured using a high temperature combustion technique, after acidification (Hedges and Parker 1976). Hydrologic characteristics measured simulta-

neously with collection of benthic samples at each site included salinity, temperature, dissolved oxygen and pH (Hydrolab Surveyor 6).

In conjunction with core sampling, sediment ammonia-nitrogen flux and oxygen uptake at all stations were measured for at least a 3 hr period using an opaque fiberglass chamber placed *in situ* by SCUBA, that covered 0.07 m^2 of bottom and contained 18 L of continuously mixed water (Flint and Kamykowski 1984). Initial triplicate 60 ml water samples were taken from the chamber for ammonium-nitrogen measurements using acid-washed PVC syringes. Continuous oxygen measurements were made with a shipboard YSI Model 57 oxygen meter connected to a chamber probe via cable. Oxygen concentrations never decreased below 4.0 ml/l (Fillos and Molof 1972). After incubation, final triplicate water samples were again removed from the chamber. Ammonium-nitrogen samples were immediately preserved with phenol (Degobbis 1973) and analyzed in the laboratory as soon as possible (Solorzano 1969). Ammonium was focused upon here because it is the preferred nitrogen form of phytoplankton (Eppley, Packard and McIssac 1970; McCarthy and Eppley 1972) and nitrate concentrations were usually low (< 0.5 μg-atm). Flux of oxygen and ammonium at the sediment-water interface were estimated according to procedures of Hargrave and Connolly (1978), after verifying the assumptions of Zeitzschel (1980) for this procedure.

Benthic compositions were compared using cluster analysis (Flint and Younk 1983) to distinguish differences in community structure among stations. To reduce heterogeneity effects the fourth-root transformation of species abundances was applied (Downing 1979), based upon previous experience with benthic analysis in this estuary (Flint and Younk 1983). Biotic characteristics in the study results were contrasted with each other and with habitat variables using Pearson correlations and multiple step-wise regression analyses (Sokal and Rohlf 1969). Analysis of variance was used to test for spatial and temporal differences among various study results.

Because of the multivariate nature of this study and the fact that many of biological variables might exhibit differing patterns between stations in the estuary, obscuring correlated patterns, it was thought that single variable analysis could provide only limited information concerning integrated characterization of these study sites. To obtain a composite description of the estuary with respect to differentiation according to the benthos and its environment at each site, multiple discriminant analysis was employed following the methods of Flint (1981). This analysis was applied to a data set consisting of benthic community structure variables and process measures of the four stations studied plus several abiotic measures characterizing each site's habitat.

RESULTS

HABITAT CHARACTERIZATION

Table 1 illustrates the long-term mean differences in habitat among study sites that characterized this coastal estuary. There was a considerable depth range. Hypoxia was never observed and water column stratification was rare, only occurring at Station 10. Station 2 salinities ranged from 5–34 ppt while at the other end of the estuary, Station 10 salinities varied from 22–35 ppt.

Station 2 was characterized by sediments comprised of 49% sand (Table 1), a considerable amount of shell (23%), and an average depth of oxygenated sediments of 2.4 cm (RPD depth). The average water content of these sediments was 57.4% by weight, the sediments contained 0.26% organic carbon by weight, and the phytoplankton production rate in this region of the estuary averaged 282.7 mg $C/m^2/d$. The middle-estuary sites

TABLE 1

Mean values (plus standard errors) for several variables that describe the environment of each station sampled along the estuarine-coastal gradient in the Corpus Christi Bay estuary.

Station	Water Depth (m)	Salinity (ppt)	Sediment Sand (%)	Sediment Water (%)	Sediment Carbon (%)	Sediment RPD Depth (cm)	Phytoplankton Production (mg $C \cdot m^{-2} \cdot d$)[a]
2	1.5	22.5 (9.2)	49.0 (1.7)	37.4 (1.5)	0.26 (0.02)	2.4 (0.3)	282.7 (66.4)
7	4.2	28.2 (2.8)	1.5 (0.3)	66.9 (1.6)	1.08 (0.03)	4.2 (0.9)	559.2 (88.2)
9	1.5	27.0 (4.1)	93.9 (0.1)	20.7 (0.4)	0.05 (0.01)	2.8 (0.3)	496.9 (78.7)
Coastal 10	12.6	31.3 (2.9)	95.2 (1.4)	21.7 (0.7)	0.05 (0.01)	3.3 (0.5)	658.7 (115.4)

[a] Data from Flint (1984)

differed mostly with respect to sediment structure (Table 1). Station 7 sediments contained large amounts of clay (76%) while water and organic carbon were high and the oxygenated sediment depth was greater than at any other site. Station 9 sediments had a high sand content with corresponding low water and organic carbon and the oxygenated sediment depth was similar to Station 2 (Table 1). There was no significant difference noted between average phytoplankton production rates at Stations 7 and 9 but these middle-estuary production measures were much greater than observed for Station 2. Station 10, sediment characteristics were similar to Station 9 (Table 1), with the exception of a slightly deeper RPD. Phytoplankton production rates in these waters were greater than at any other site.

BENTHIC COMMUNITY STRUCTURE

Benthic macroinfaunal taxa number showed a significant ($P < 0.05$) increase from the fluvial-influenced upper-estuary moving toward the coastal habitat of Station 10 (Fig. 2). A greater number of taxa were usually observed at the sandier sites (*i.e.* Stations 9 and 10). Station 2 exhibited consistent winter-spring peaks in number of taxa but this pattern was lost at the other sites. Unlike the other 3 sites, Station 7 exhibited a continuous increase in taxa over the study duration. During initial intervals benthic taxa numbers were low (Fig. 2). After January 1982, taxa steadily increased to

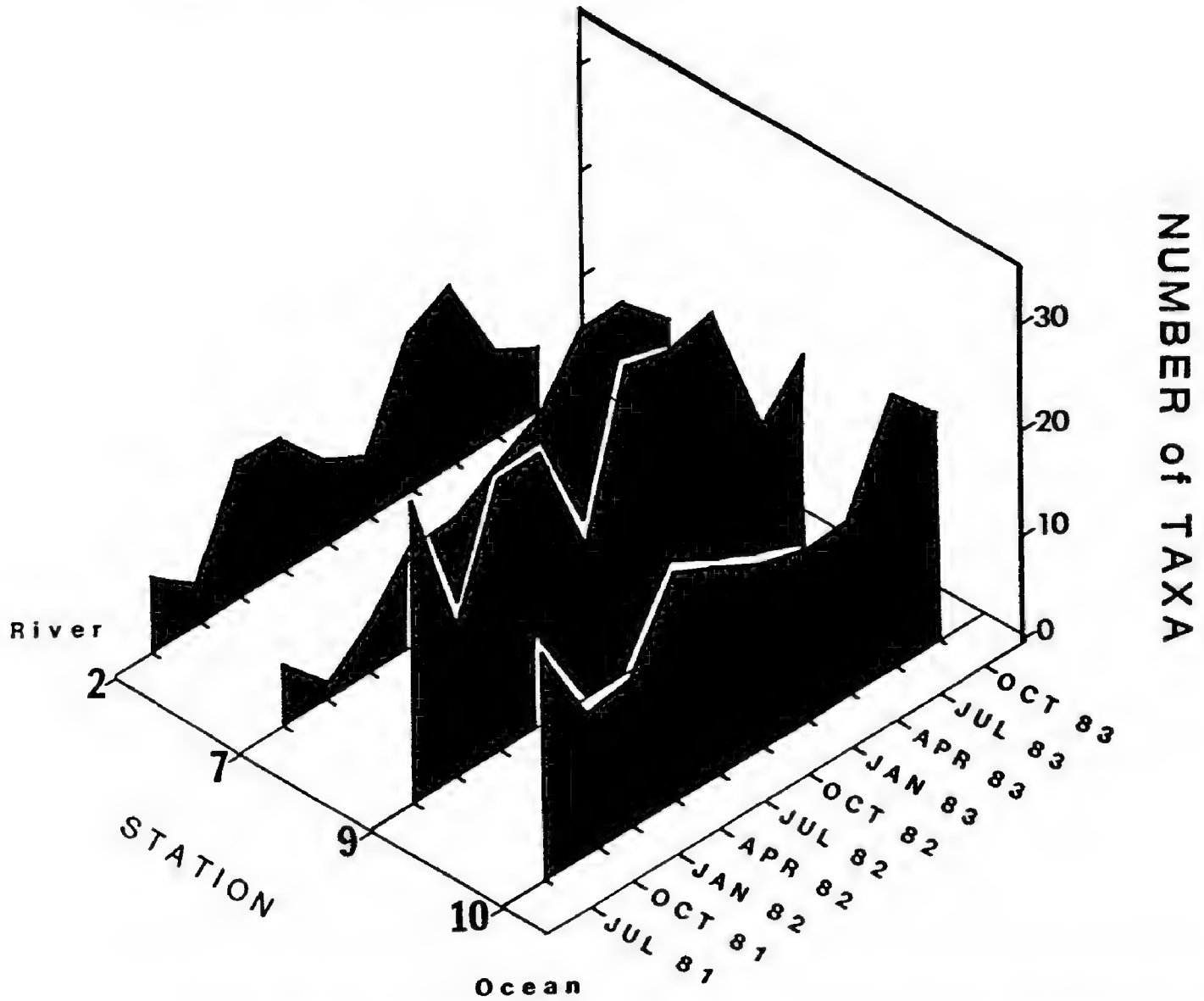


FIG. 2. Temporal and spatial patterns in benthic macroinfaunal taxa number measured for the Corpus Christi Bay estuary sampling sites.

maximum measurements at the end of the investigation. There were no seasonal patterns.

Benthic macroinfaunal abundance exhibited significant differences ($P < 0.01$) between the four study sites in Corpus Christi Bay (Fig. 3). Over the entire study greatest abundances occurred at Station 7. Station 2 also exhibited higher benthic macroinfaunal abundances than either Station 9 or Station 10. Peaks in abundance were not consistent in time among the sampling sites. The only repeating seasonal pattern was at Station 9 where peaks occurred in the winter and spring (Fig. 3). Spring 1982 peaks in abundance at Station 7 shifted to the summer in 1983. Winter-spring maxima were observed at Station 2 in 1983 but no similar trend occurred in 1982.

Vertical distribution of benthic taxa within the sediments at each study site was similar with the exception of Station 7. Collections from Stations 2, 9, and 10 routinely showed that greater than 90% of the benthic macroinfauna taxa and more than 93% of the total benthic community abundance occurred in the top 3 cm of sediment. Station 7 collections showed similar

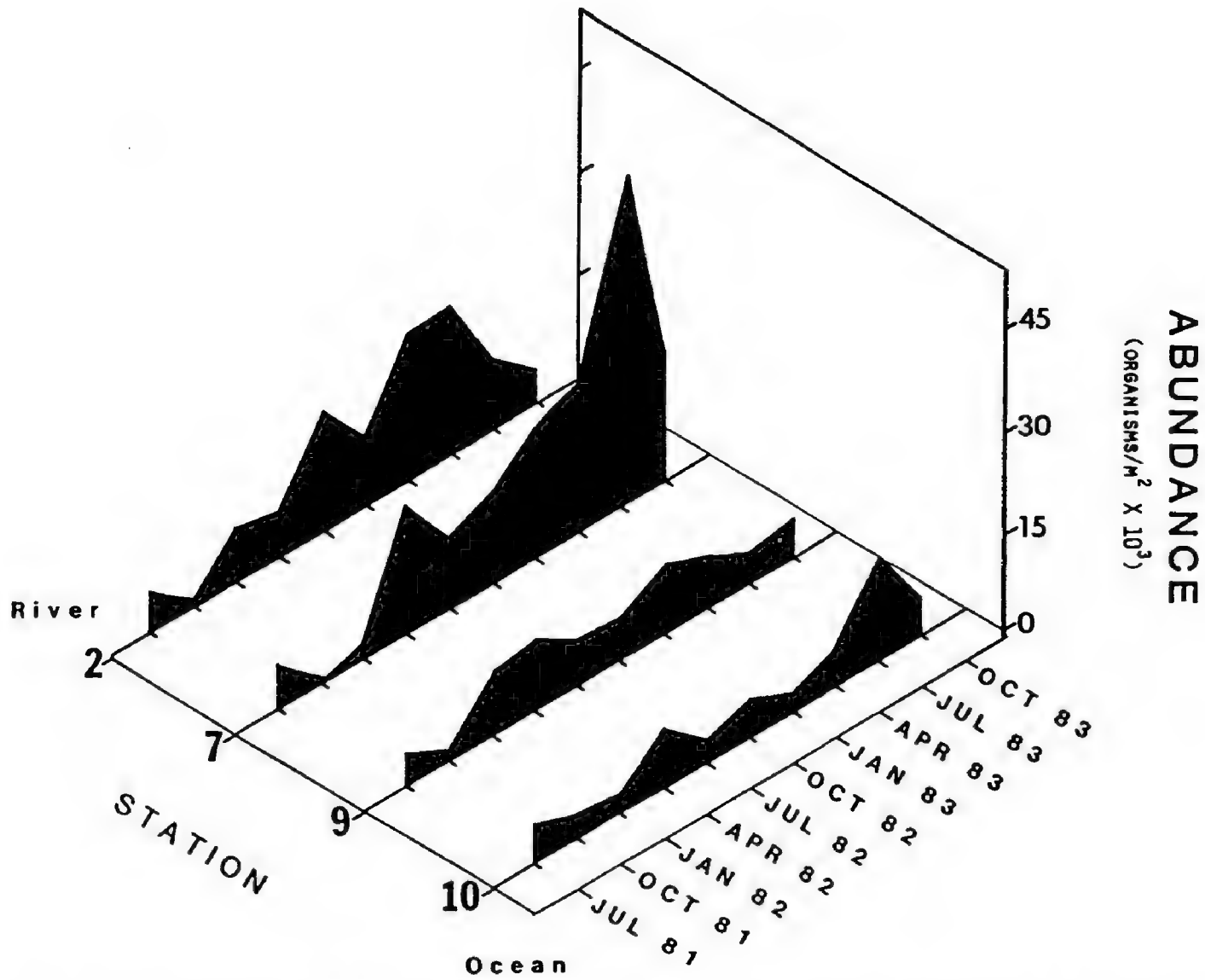


FIG. 3. Temporal and spatial patterns in benthic macroinfaunal total abundance measured for the Corpus Christi Bay estuary sampling sites.

patterns through January 1982. After this collection period, however, the species of acorn worm, *Schizocardium* sp., colonized the muds at this site, burrowed deep into the sediments (> 0.5 m), and enhanced deeper migration by other infaunal inhabitants, as described elsewhere (Flint and Kalke, in preparation). As a result vertical distribution of benthic macroinfauna was much more even throughout the top 30 cm at Station 7 after April 1982.

Higher abundances and lower taxa number, which were observed in the less saline, more variable regions of the estuary, in contrast to the more oceanic regions, suggested that species diversity might exhibit spatial trends. Therefore, the Shannon-Wiener diversity measure (Pielou 1966) was examined. From Station 2 through Station 10 average species diversity measures over the entire study period were 1.9, 1.7, 3.5, and 3.4, respectively. The further away from the fluvial influence to the estuary and the higher the sediment sand content (Table 1), the greater the species diversity of the benthos.

Cluster analysis was used to differentiate species assemblages. Lack of station overlap within the major clusters of the dendrogram (Fig. 4)

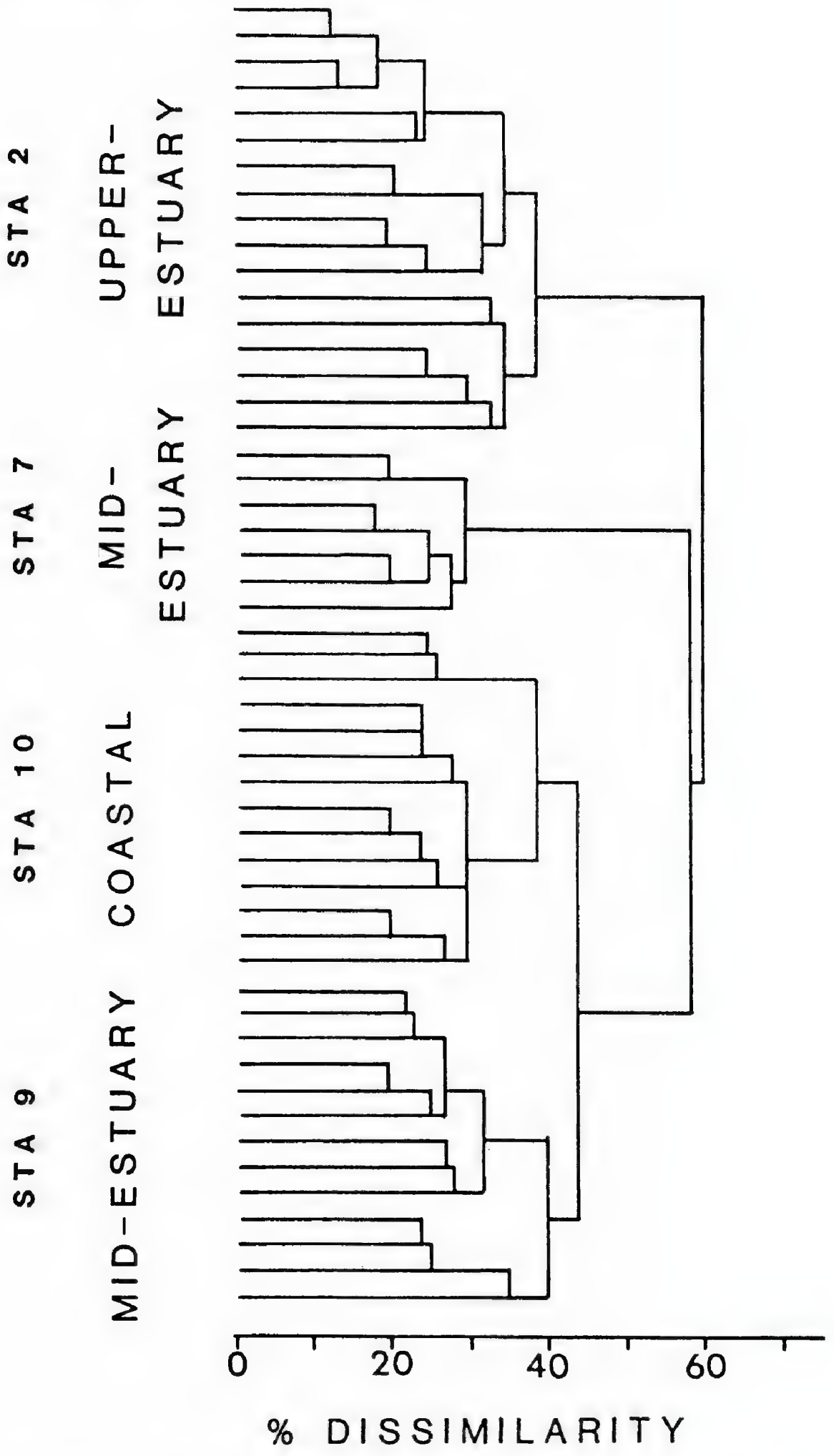
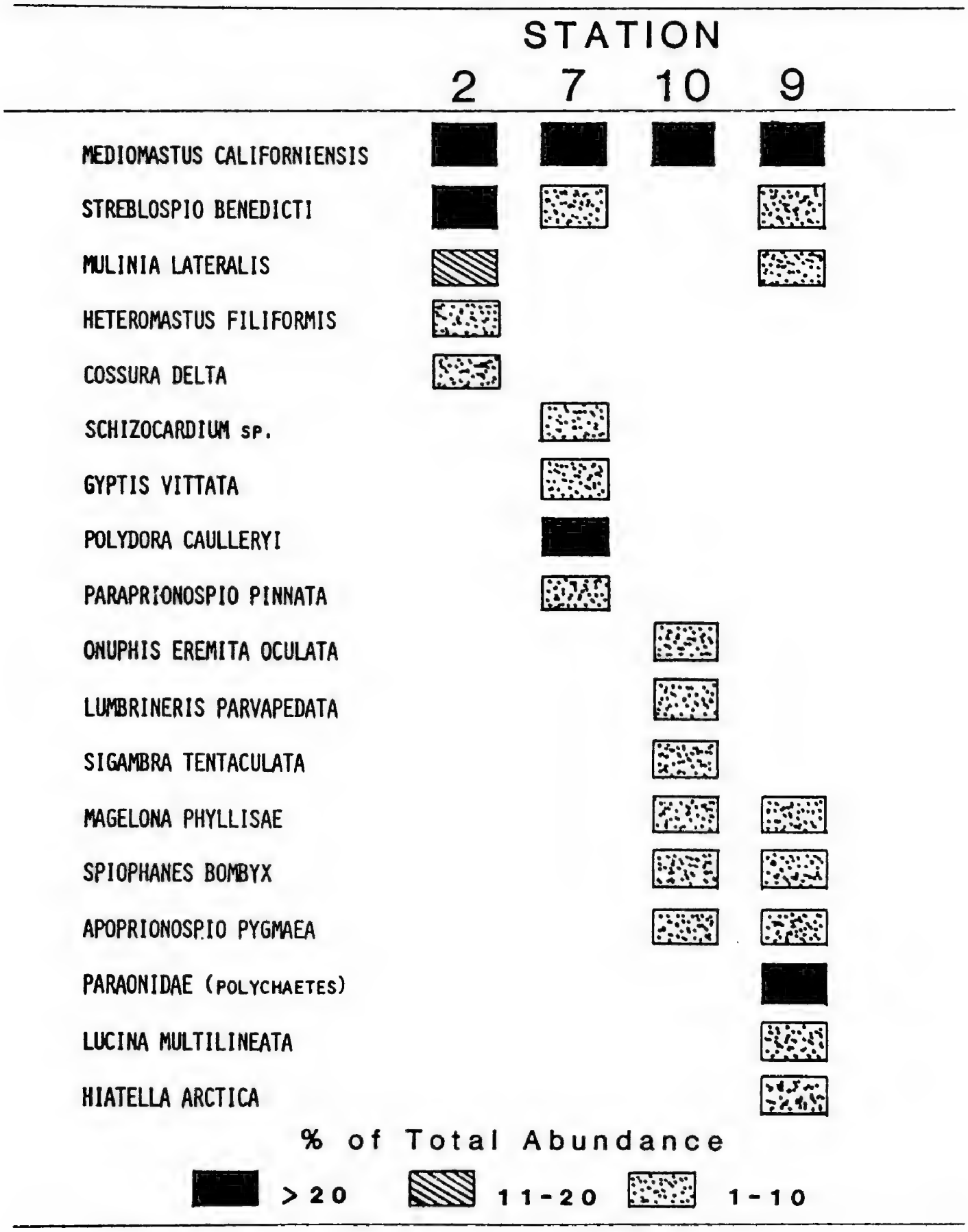


FIG. 4. Benthic macroinfaunal community differentiation in Corpus Christi Bay as determined by cluster analysis of species assemblages, for each sampling date/station.

indicated that each of the sites was different in overall species assemblage. Station 2 was most unlike any of the other collection sites. Although all study sites supported dominant populations of the small, burrowing polychaete *Mediomastus californiensis* (Table 2), Station 2 supported much greater

TABLE 2

Distribution of dominant benthic macroinfaunal species at the four stations along the estuarine-coastal gradient in the Corpus Christi Bay estuary.



populations of *Streblospio benedicti* and larger numbers of the bivalve *Mulinia lateralis* than any of the other sites. In addition, the polychaetes *Heteromastus filiformis* and *Cossura delta* were only observed at Station 2.

Station 7 was different in benthic community structure from Stations 9 and 10 at a dissimilarity level of 58% (Fig. 4). This station supported populations of *M. californiensis* and *S. benedicti*, as did other sites (Table 2). Populations of the acorn worm *Schizocardium* and the polychaetes *Gyptis vittata*, *Polydora caulleryi*, and *Paraprionospio pinnata*, however, were only observed at this middle-estuary site consistently and *P. caulleryi* along with *M. californiensis* dominated in the community.

Stations 9 and 10 were most alike in community structure (Fig. 4). Part of this similarity was because of the common occurrence of several polychaete species at both sites (Table 2). The polychaete *S. benedicti* and the bivalve mollusc *M. lateralis* were not observed beyond the confines of the barrier island, however, and did not occur at Station 10, causing one difference in benthic community structure between these sites. Another difference was the large abundance of polychaetes classified as paraonids at Station 9 and the absence of this faunal group at Station 10 (Table 2). Station 10 also showed more even distributions between taxa with only one species comprising more than 10% of total community abundance.

With the exception of Station 9, benthic macroinfaunal biomass showed seasonal peaks at the study sites in Corpus Christi Bay (Fig. 5). Peak biomasses were observed at station 2 in the spring of each year. At Station 7 peak biomass occurred later than at Station 2, during the summer period. This site showed a pattern for biomass similar to abundance trends (Fig. 3) during the study period. After January 1982, *Schizocardium* sp. colonized these sediments and growth for this large-sized population accounted for much of the increased benthic biomass that was observed (Fig. 5). The smaller biomass maxima that were observed at Station 9 occurred during the winter in 1982 and during the spring in 1983. Most distinct peaks in biomass occurred at the coastal site, Station 10, in April of each year. Burrowing anemone populations that were large in size and occurred at this site only during the spring sampling intervals caused these peaks. For example, greater than 70% of total biomass at Station 10 during April intervals was represented by anemone populations with 1 or 2 individuals occurring in each set of triplicate cores.

Vertical distributions of benthic macroinfaunal biomass paralleled those patterns observed also for taxa number and total abundance. Stations 2, 9, and 10 consistently exhibited peak biomasses in the top 3 cm of sediment. In contrast, Station 7 infaunal biomass peaks often occurred at depths greater than 10 cm after the April 1982 colonization by *Schizocardium* populations. Station 7 collections exhibited largest mean wet weight biomass for the study period at 86.4 g/m^2. Station 10 showed high mean biomass (85.1 g/m^2) if the few anemone occurrences were included. Excluding anemones Station 10 mean biomass was 22.6 g/m^2. Station 2 exhibited a study mean of 49.0 g/m^2 for benthic biomass while Station 9 showed a study mean of 25.5 g/m^2.

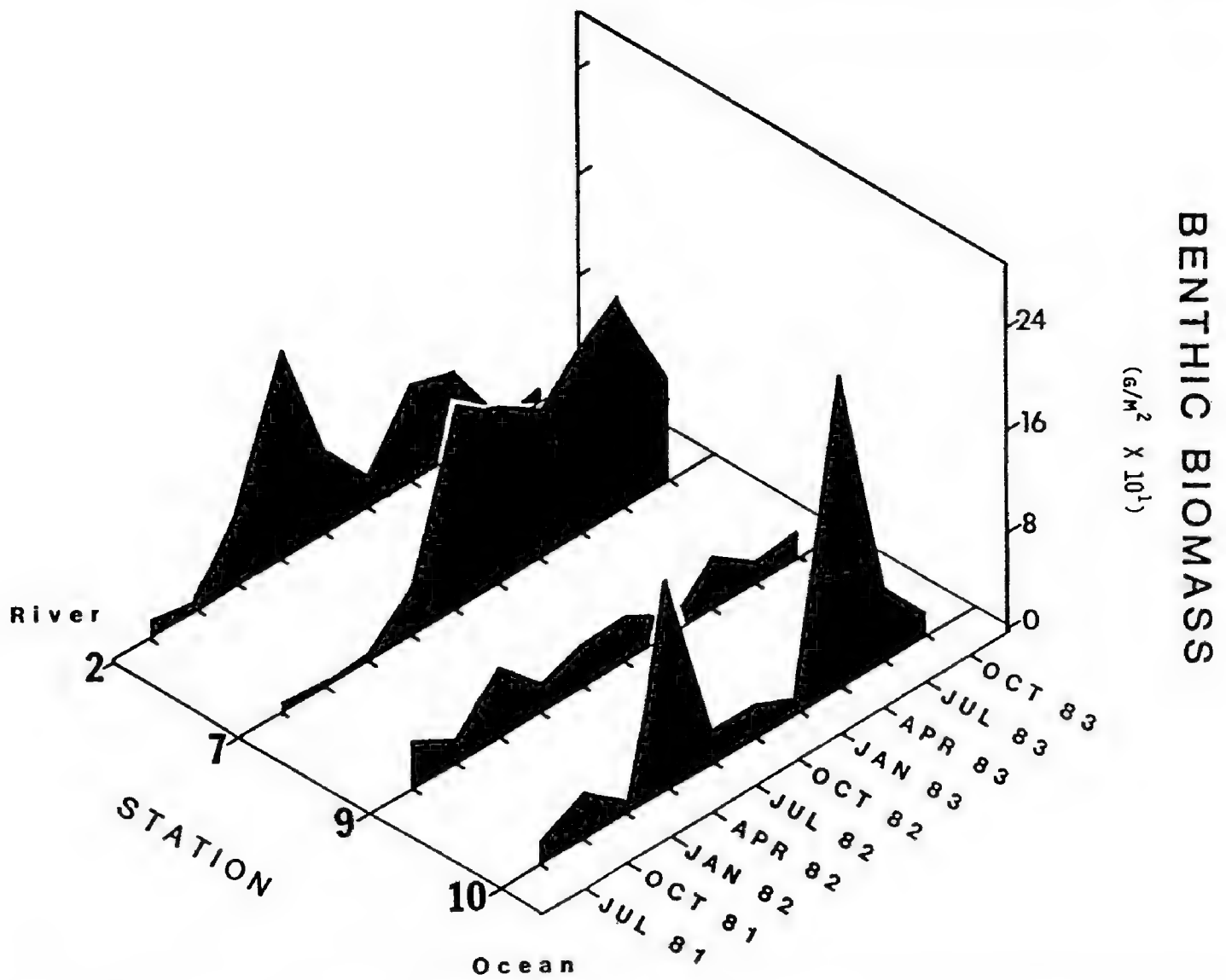


FIG. 5. Temporal and spatial patterns in benthic macroinfaunal total wet weight biomass measured for the Corpus Christi Bay estuary sampling sites.

BENTHOS FUNCTION

There was very little regular temporal or spatial pattern observed concerning benthic community metabolism in the Corpus Christi Bay estuary (Fig. 6). During the study period, mean metabolic rates for collection sites from river-influenced to oceanic-influenced ends of the estuary (Stations 2–10) were 130.6, 125.7, 123.6, and 101.6 ml $0_2/m^2/h$ respectively. There was no significant difference observed among these measures. At Station 2, higher metabolic rates (Fig. 6) were most closely associated with lower salinities ($r = -0.68, n = 14$), when high rainfall and fluvial flow rates were observed in July 1981 and July–October 1983 (Flint 1984). At Stations 7 and 9 the increased metabolic rates that occurred paralleled corresponding increased benthic biomass at these sites (Figs. 3 and 5), exhibiting a significant ($P < 0.01$) correlation of $r = 0.63$ ($n = 22$).

Of all the benthic variables measured during this study, benthic ammonium regeneration rates showed the most distinct seasonal pattern (Fig. 7). All study sites exhibited peak regeneration rates during July of each year. In some cases the July maxima were either preceded or followed (April or October) by very high rates, but the general pattern was peak sediment

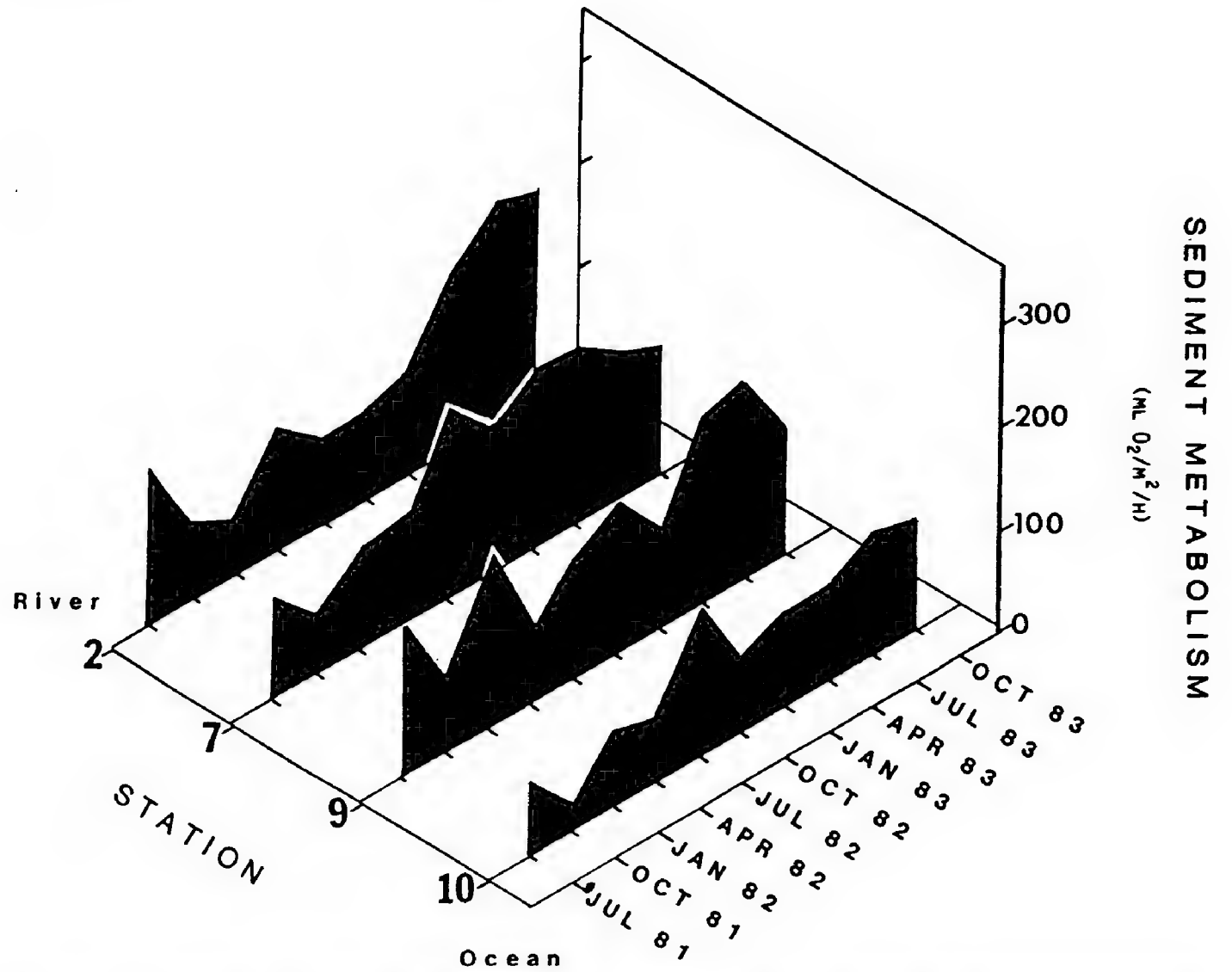


FIG. 6. Temporal and spatial patterns in sediment metabolism measured for the Corpus Christi Bay estuary sampling sites.

recycling of ammonium during the summer in the Corpus Christi Bay coastal ecosystem. According to ANOVA, no significant spatial variation in benthic regeneration rates was observed among the 44 measures at the 4 sites. Although there were definite decreases in total study period average rates from a high at Station 2 of 160.2 μg-atm NH_4^+–$N/m^2/h$ to a low at Station 10 of 89.2 μg-atm NH_4^+–$N/m^2/h$, temporal variability within collection sites was great enough to prevent analysis of variance from detecting significant differences among sites. There was no significant relationship observed between benthic nutrient regeneration rates at the four sites and measurements of sediment oxygen demand during the total study period in the Corpus Christi Bay ecosystem.

BENTHOS STRUCTURE AND FUNCTION INTEGRATION

Graphic results of the multivariate discriminant analysis, employed to integrate the benthos community variables over the spectrum of environmental variation, are illustrated in Fig. 8. Calculated F statistics between

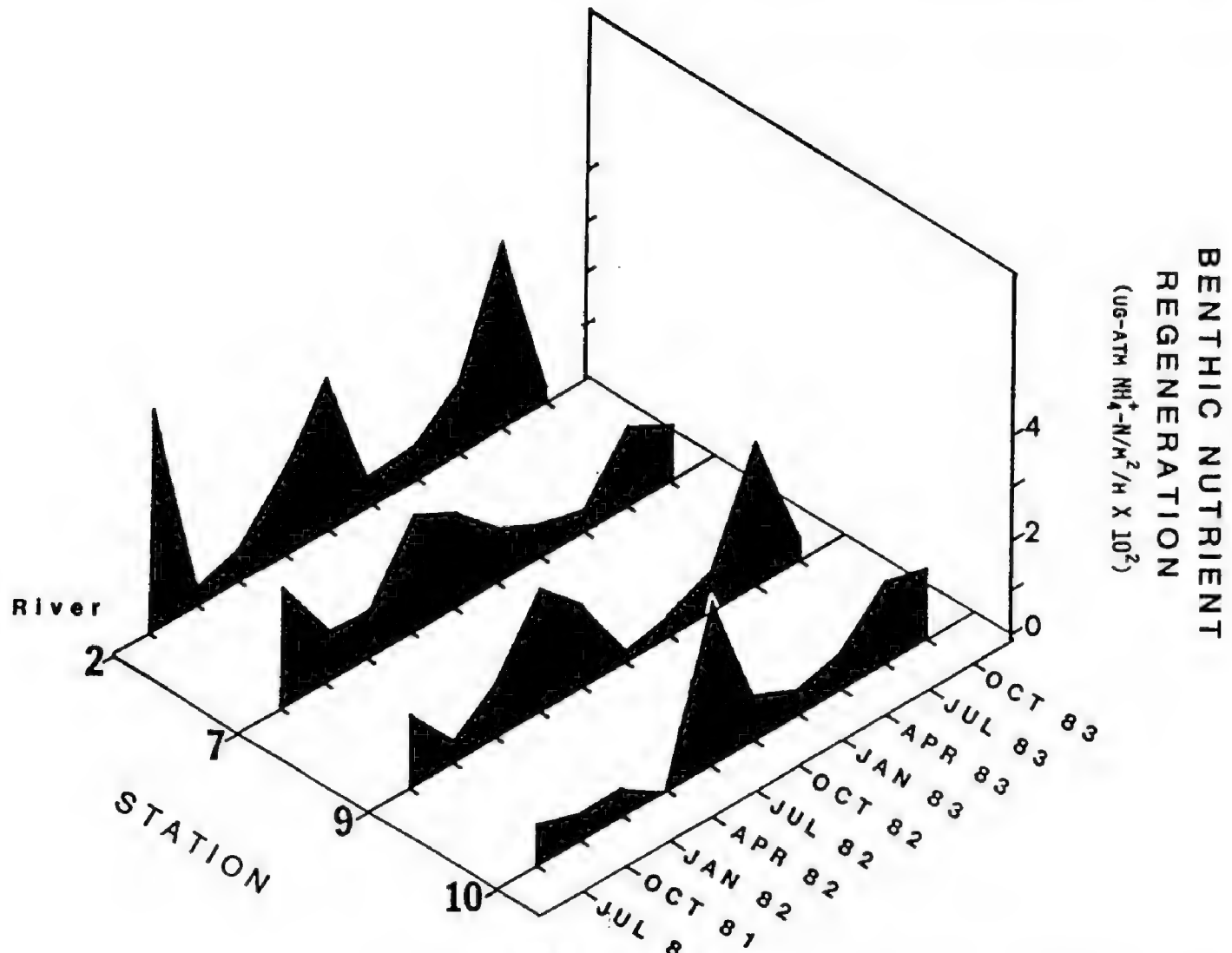


FIG. 7. Temporal and spatial patterns in benthic nutrient regeneration measured for the Corpus Christi Bay estuary sampling sites.

each pair of stations in the estuary indicated that a significant difference ($P < 0.01$) existed among all sites when the discriminant functions included the following variables: station salinity variance, sediment sand content, sediment organic carbon content, benthic taxa number, and sediment metabolism. The first discriminant function (Fig. 8) explained 82% of the variation among stations. Variance in bottom water salinity at each site, which was directly related to water depth of the station, was the most significant discriminating variable on the first function and differentiated Station 10, the deepest study site, from Station 7 and Station 7 from Stations 9 and 2, the shallowest study sites. Benthic taxa number also exhibited a large standardized coefficient for the first discriminant function. This function distinguished among habitats where a less variable environment supported a larger number of taxa in the benthic community (*e.g.*, Station 10).

The second discriminant function (Fig. 8) was able to explain an additional 17% of variance among study sites and significantly distinguished differences for Stations 2, 7, and 9. The most significant discriminating variable for this function was the difference in sediment structure among

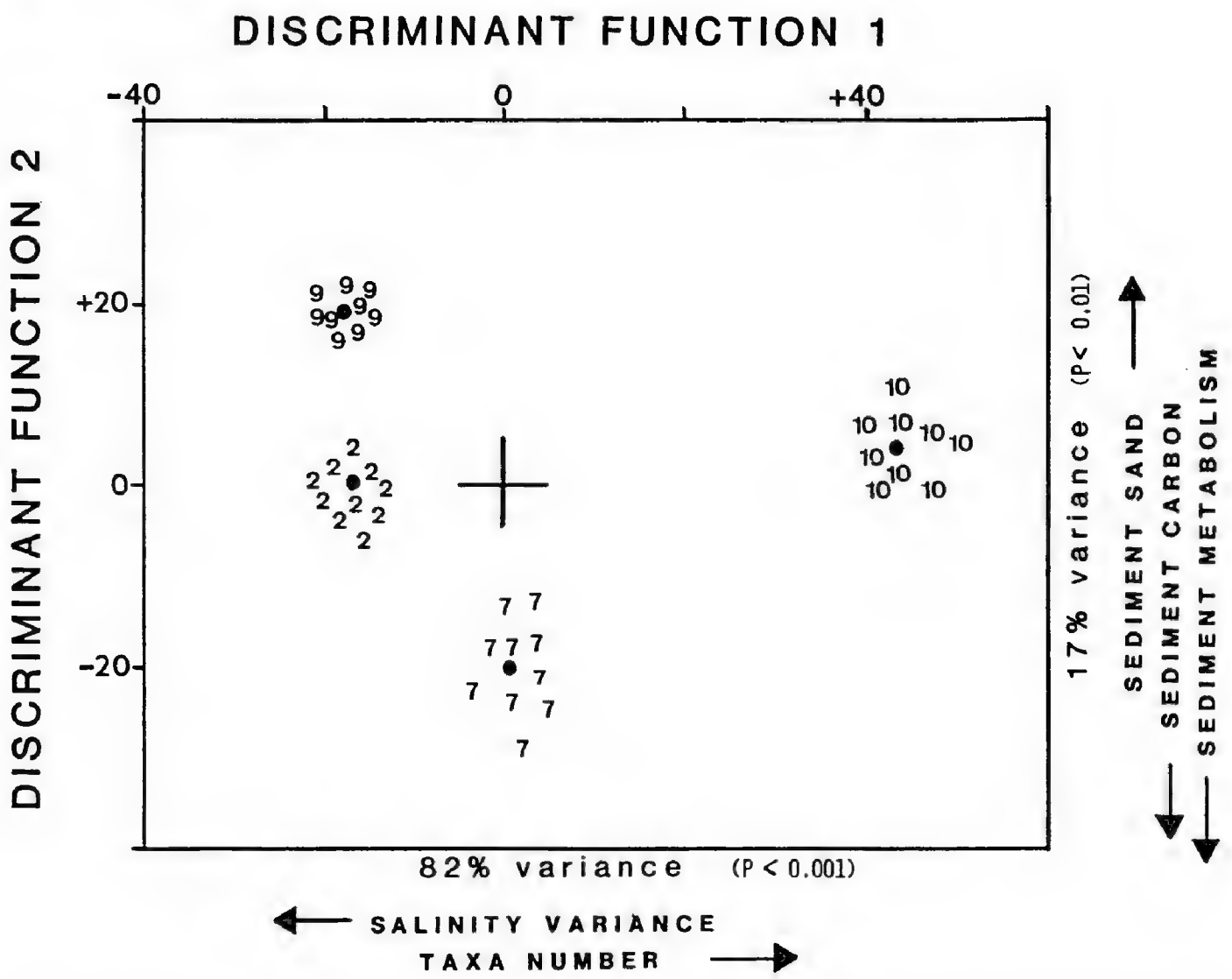


FIG. 8. Discriminant analysis results comparing abiotic factors with benthic structural and functional variables from this study. The amount of variance that each discriminant function explains in the data is illustrated together with those variables exhibiting the largest coefficients for each function along with their direction of change. Each station sample in the plot is represented by its station number, along with the mean for that station.

sites, as characterized by percent sand. Corresponding with differences in sediment texture were differences in the amount of sediment organic carbon content measured at each site, where Station 7 exhibited the greatest measures followed by Station 2 (Table 1). Another variable represented by a relatively high coefficient for the second discriminant function was sediment metabolism. Station 7 exhibited greatest measures which were correlated ($r = 0.76$) to larger benthic biomass values at this site. Thus, discriminant analyses characterized a site (Station 7) whose sediment was characterized by a lower sand content that was less stable and easily resuspended by bottom currents, which was inhabited by fewer benthic taxa. This was in contrast to more sandy sediments at Stations 2 and 9 that supported higher taxa numbers. Station 7 also had a greater sediment food content (organic carbon measure) which was related to greater community biomass (Fig. 5) and higher sediment metabolism (Fig. 6) than the other sites, especially Station 9.

DISCUSSION

Differences in the benthos of Corpus Christi Bay estuary were accompanied by changes in the physico-chemical nature of the habitat. Riverine-influenced and oceanic-influenced stations exhibited distinct community structures, characterized by differences in species composition (Fig. 4 and Table 2), taxa number (Fig. 2), abundance (Fig. 3), biomass (Fig. 5), and species diversity. Generally, the upper-estuary had an intermediate grain-size sediment with a relatively shallow RPD layer and low phytoplankton production. Greatest variability in salinity was observed in the upper-estuary (Table 1) and sediment organic carbon was mid-range relative to other sites. The deeper, middle-estuary region (Station 7) was characterized by very fine (clay) organically-rich sediments with a much greater RPD layer depth. The lower-estuary (Station 9) and coastal waters (Station 10) contained coarser, less organic sediments with mid-range RPD layer depths relative to other sites. Primary productivity was greatest in the coastal waters (Table 1; Flint 1984) and salinity variability was much less than in the upper-estuary.

The upper-estuary was dominated by species such as *Mulinia lateralis* and *Heteromastus filiformis*, which are thought to have low competitive fitness, but thrive where adverse conditions, such as highly reducing sediment or extreme salinity fluctuations, exclude other organisms (Holland, Maciolek and Oppenheimer 1973; Parker 1975; Shaffer 1983). The more reduced sediments and highly variable salinities of the upper-estuary were associated with lower taxa numbers and dominated by a few species which contributed to greater abundance and biomass in these sediments. Species inhabiting the lower-estuary and coastal waters, such as the polychaetes *Magelona phyllisae*, *Spiophanes bombyx* and *Aproprionospio pygmaea*, generally are not as tolerant of rapid salinity changes and prefer sandier more highly oxygenated sediments, lower in organic content. Greater species richness, more community diversity and lower total abundance and biomass were associated with these higher, less variable salinities and sandier sediments of the lower-estuary.

The results of these investigations demonstrate how essential it is to consider the physical-chemical gradation that is characteristic of many estuaries from their fresh to saline water sources when one wishes to assess the importance of the benthos to the ecosystem. Estuarine segmentation often results in the characterization of zones correlated with gradient environmental variations (*e.g.*, Carriker 1967, Tenore 1972, Wolff 1973, Boesch 1973). Implicit in the long-standing perception of this estuarine segmentation is the existence of biotic discontinuities, or zones of abrupt biotic change, where a similarity in community composition, structure, and function is assumed within the zone (Boesch 1977). Thus, in assessing the overall role of the benthos, the variability associated with estuarine environmental changes, as was observed in this study, must be integrated in order to more adequately assess the contributions of the benthos to the entire ecosystem, supporting important fisheries. Sampling in only one of the biotic

zones will not provide adequate characterization of the benthos' importance throughout the estuary.

Increased sediment ammonium regeneration rates appeared to be related to periods of high freshwater input to the upper-estuary of Corpus Christi Bay. Two periods of high freshwater flow occurred in this estuary, in July 1981 and July through October 1983 (Flint 1984). Both of these intervals represented peak periods of ammonium-nitrogen flux from the sediments at Station 2 (Fig. 7). In contrast, measurements made further away from the riverine input indicated that the relationship between salinity and ammonium flux rates became weaker. For example, correlation analyses between ammonium regeneration and salinity showed the following: Station 2, $r = -0.61$; Station 7, $r = -0.58$; Station 9, $r = -0.40$; Station 10, $r = -0.03$. Besides suspected effects of bioturbation on sediment nutrient fluxes, a process suggested as being very important in estuarine environments that undergo sudden salinity changes is the convective, density-gradient driven overturn of sediment pore water (Lindberg and Harriss 1973, Edwards 1981). During periods of abrupt salinity change a density gradient is established between the sediment pore water and bottom waters above the mud-water interface. This gradient is thought to drive diffusional processes, pumping nutrient-rich pore waters out of the sediments. Edwards (1981) suggested that sudden salinity transitions should have the greatest functional impact when they occur in the more oligohaline portions of the estuary, because density changes are larger and more frequent. This is consistent with data presented here.

The shallowness of Corpus Christi Bay permits a close coupling between sediments and overlying waters, allowing the benthos to serve as a pivotal link in the function of this estuary. The benthos can act as an efficient "trap" capturing energy from different materials flowing through the estuary (*i.e.* phytoplankton, terrestrial detritus, estuarine detritus), concentrating this energy into biomass ready for consumption by secondary consumers. Flint and Rabalais (1981) illustrated that as much as 80% of annual pelagic organic material was diverted to the benthos in shallow south Texas coastal waters. This organic material potentially has three fates once it reaches the sediment surface: food for benthic fauna, carbon substrates for remineralization by bacteria, and burial.

The conversion of Corpus Christi Bay mean sediment metabolism (from all measurements during the study) to carbon equivalents, assuming 1 ml O_2 equals 0.456 mg C (Rowe and Smith 1977), indicated that the benthos can produce 509 g C/m^2/y. This production appears quite high when considering mean phytoplankton production in Corpus Christi Bay is 175 g C/m^2/y (Flint 1984). Considering the other uses of phytoplankton carbon production in this estuary besides the benthos, it can be assumed that there are probably a number of other carbon sources to the benthos, besides phytoplankton. The benthic production rate estimated for Corpus Christi Bay fell midway between estimates of 876 g C/m^2/y for the Georgia Coastal Bight (Hopkinson and Wetzel 1982), 620 g C/m^2/y for the Neuse River Estuary (Fisher, Carlson

and Barber 1982), 307 g C/m^2/y for Narragansett Bay (Hale 1975; Furnas, Hitchcock and Smayda 1976), 164 g C/m^2/y for Loch Thurnaig (Davies 1975), and 55 g C/m^2/y for Buzzards Bay (Rowe, Clifford, Smith and Hamilton 1975).

Another aspect of the pivotal link the benthos provides in the Corpus Christi Bay estuary is related to its role in sediment nutrient recycling. Pooled measurements from all stations in the estuary indicated that 2.9 mg-atm NH_4^+–N/m^2/d were recycled by the benthos. This mean regeneration rate was similar to measures for many other estuaries where data existed. For example, average daily rates of ammonium regeneration for other estuaries included, 1.0 mg-atm/m^2/d for Loch Thurnaig (Davies 1975), 1.3 mg-atm/m^2/d for Buzzards Bay (Rowe *et al.* 1975), 2.1 mg-atm/m^2/d for Narragansett Bay (Hale 1975, Furnas *et al.* 1976), 3.0 mg-atm/m^2/d for the Patuxent Estuary (Boynton, Kemp and Osborne 1980), and 5.4 mg-atm/m^2/d for the Neuse River Estuary (Fisher *et al.* 1982).

The importance of these regeneration rates are most obvious when compared to the requirements of autotrophs needing nutrients for photosynthesis. Using measured rates for phytoplankton production in Corpus Christi Bay (Flint 1984) and calculating nitrogen demand from a C:N ratio of 6.6 (Redfield, Ketchum and Richards 1963), it was estimated that sediment recycling could provide approximately 81% of the nitrogen needed to support annual phytoplankton production rates. A breakdown by station of these data in the estuary indicated that all site sediments except the coastal station (Station 10) supplied more than 60% of phytoplankton-needed nitrogen.

Fig. 9 presents an integrated summary of selected measurements characterizing benthic communities in Corpus Christi Bay, along with 10 year averages for shellfish and finfish fishery yields in this estuary (G. Kinkle, NOAA, NMFS, Miami, Florida, personal communication, 1983). The relative synchrony in cycles for these various components and processes is of interest even though it is acknowledged that quarterly observations may not provide a complete picture of annual cycles for this estuary. Peaks in benthic biomass were observed in the spring (Fig. 9), during periods when shrimp and finfish populations were at their maximum and would require substantial food. Over a 10 year period in this estuary a correlation of $r = 0.82$ was observed between annual benthic biomass and annual shrimp fishery harvest (Flint 1985). Annual peaks in phytoplankton production and benthic carbon production, as calculated for O_2 metabolism measures (see above), also corresponded reasonably well. Both exhibited increases in spring and maxima in the summer in Corpus Christi Bay (Fig. 9). Thus, the general temporal correspondence among primary production, benthic biomass and carbon production, and fisheries yields emphasized these key trophic connections in the Corpus Christi Bay estuary.

Comparing temporal trends in ammonium regeneration by the benthos and phytoplankton production further indicated the strong coupling between these two processes (Fig. 9). Both benthic regeneration rates and

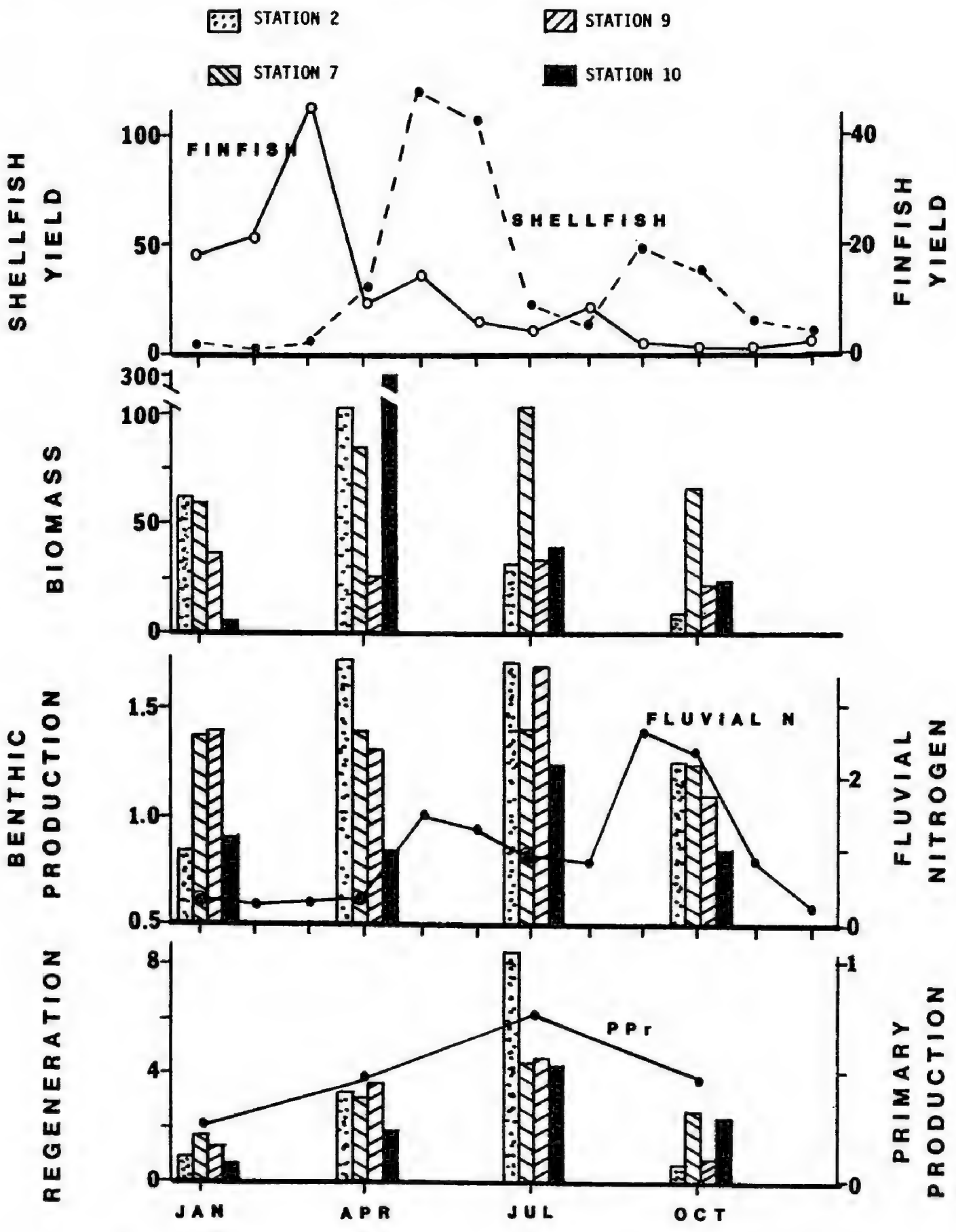


FIG. 9. The integration of all benthic study results along with fishery yields (kg × 10^3), fluvial nitrogen input to the estuary (kg/d), and phytoplankton production (g C/m^2/d). Benthic biomass units are g/m^2, benthic production of carbon (see text) is expressed as gC/m^2/d_2 and benthic nutrient regeneration units are mg-atm NH_4^+–N/m^2/d.

phytoplankton production were greatest at all stations in the summer. In contrast, nitrogen supplies from the fluvial input to the estuary (Texas

Department of Water Resources 1981) were low during the summer, with maximum input during the fall (Fig. 9), when primary production rates were decreasing. Phytoplankton production dynamics more closely paralleled benthic ammonium regeneration than nitrogen supplies from the fluvial flow to Corpus Christi Bay. This integrated summary demonstrated the importance of the benthos to this estuary as well as probably many other Gulf coast estuaries.

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ZOOPLANKTON DISTRIBUTION IN A WIND-DRIVEN ESTUARY BEFORE AND AFTER A MAJOR STORM

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ABSTRACT

Storm effects on zooplankton distribution were assessed in Calcasieu Lake, a very shallow, well-mixed estuary in which strong winds override tidal flow, and salinity is strongly influenced by freshwater inflow. Wind speeds up to 30 m/sec and 150–200 mm of rainfall were recorded in this area as Tropical Storm Chris moved inland on September 11, 1982. Sampling was conducted two days prior to the passage onshore of the tropical-storm center, and repeated two days after the storm. Salinity decreased and temperature increased in the estuary after the storm. We identified concurrent changes in zooplankton abundance. Significantly lower abundances were recorded after the storm for several zooplankton taxa, including: larval and postlarval *Anchoa* spp., larval and postlarval Sciaenidae, total decapod zoeae, *Pinnixa* sp. zoeae, *Neopanope* sp. zoeae, and total copepods.

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INTRODUCTION

The few published studies concerned with the effects of severe storms on estuarine zooplankton (Breder 1962; Grant, Bryan, Jacobs and Olney 1974; Hawes and Perry 1978; Heinle, Millsaps and Millsaps 1974; Robins 1957; Simmons and Hoese 1960), have compared abundances over periods of years rather than identifying short-term fluctuations in abundance resulting from the immediate effects of the storm. Long-term comparisons cannot adequately separate storm effects from seasonal or inter-annual population fluctuations. Although estuarine holoplankton and meroplankton presumably are adapted to predictable seasonal changes in weather, abnormal events such as the occurrence of intense tropical storms are probably not sufficiently predictable for evolutionary response. The purpose of our study was to determine what short-term effects an unpredictable event such as a tropical storm would have on the zooplankton community of a shallow, wind-driven estuary. Specifically we wanted to see if zooplankton would be flushed out of the estuary by increased runoff or by currents driven by high winds.

MATERIALS AND METHODS

Calcasieu Lake (30°00′N, 93°20′W) is a very shallow estuary (average high tide depth = 1.5 m) connecting the Calcasieu River with the Gulf of Mexico. The lake is the largest body of water in southwest Louisiana, covering approximately 255 km^2. Previous characterization of lake hydrography (Vecchione, Lascara, Stubblefield and James 1983; Stubblefield, Lascara and Vecchione 1984) indicated a vertically well-mixed system. Randall and James (1982) found that salinity decreases up-estuary and to the east. Tidal cycles dominate circulation in the lake; however, strong winds override celestial tides resulting in longer than usual periods of outflow or inflow (Kelly, Randall and Schmitz 1982).

The Calcasieu River has been dredged to a depth of 15 m, and spoil banks have formed along the edges of the channel. These banks limit circulation between the river channel and surrounding lake (Gosselink, Cordes and Parsons 1979). Hydrologic modeling of the Calcasieu River/Lake system (James and Randall 1983) indicated that the dredged channel is a separate component of the estuarine system; salinity dynamics in the channel are dominated by riverine discharge. In addition, changes in the community structure of zooplankton in the river channel have been correlated with flow changes (Vecchione and Lascara 1983).

We sampled six stations (Fig. 1) during daytime high tide two days prior to the passage of a late-season tropical storm and again two days after it passed. Samples were collected and processed similarly on each date. Weather conditions were recorded and hydrography was profiled at each station prior to sampling. A Hydrolab Series 8000 meter was used to measure temperature, conductivity and dissolved oxygen at 1 m intervals at the deepest stations, E5 and E1. Similar measurements were made near surface and near bottom at all other stations.

At each station a triplicate series of one-minute tows was made (boat speed of 0.9–1.5 m/sec) using a one-half meter net with 0.153 mm mesh netting and soft cod end, modified to prevent avoidance due to bridle or boat wake (Stubblefield *et al.* 1984). At most stations the bottom depth was approximately 1 m and the net was towed with the mouth ring just below the surface; however, at the deeper stations, E5 and E1 (bottom depth 4–5 m), a double oblique tow from the surface to approximately 3 m and back to the surface was necessary to sample the water column adequately. The volume of water filtered by the net was estimated based on readings from a flowmeter located in the mouth of the net.

Samples were preserved in the field using a 3–5% solution of formaldehyde in seawater buffered with sodium borate. Because of requirements of the contract which funded this work, laboratory protocol emphasized fish larvae and postlarvae. Thus, within-station variability was only assessed for fishes. All fishes were identified from each sample. Decapod larvae, copepods and fish eggs were identified from the first sample of each replicate set. Due to the high abundance of decapod zoeae and copepods, subsampling with a Folsom Plankton Splitter was frequently necessary. The following groups were targeted for analysis based on their numerical dominance or commercial fishery importance: *Anchoa* spp. larvae and postlarvae; *Anchoa mitchilli* eggs; sciaenid eggs, larvae and postlarvae; total decapod zoeae; zoeae of *Pinnixa* sp. and *Neopanope* sp., total decapod megalopae; *Callinectes* sp. megalopae; total copepods; and *Acartia tonsa* adults and copepodites.

Abundances were standardized to number of individuals per cubic meter of water filtered. The non-parametric Wilcoxon Signed Rank Test (Mosteller and Rourke 1973) was used to test for statistically significant differences based on comparisons of abundance at paired stations between the two sampling dates. A two-way analysis of variance (Sokal and Rohlf 1969) was chosen for parametric comparisons of replicate fish abundances before and after the storm. When statistically significant differences between pre-storm and post-storm abundances were demonstrated by ANOVA, the Student-Newman-Keuls test (Sokal and Rohlf 1969) was employed for *a posteriori* comparisons among means to indicate the pattern of heterogeneity.

RESULTS

PHYSICAL DATA

Pre-storm sampling was conducted on September 9, 1982. Peak winds

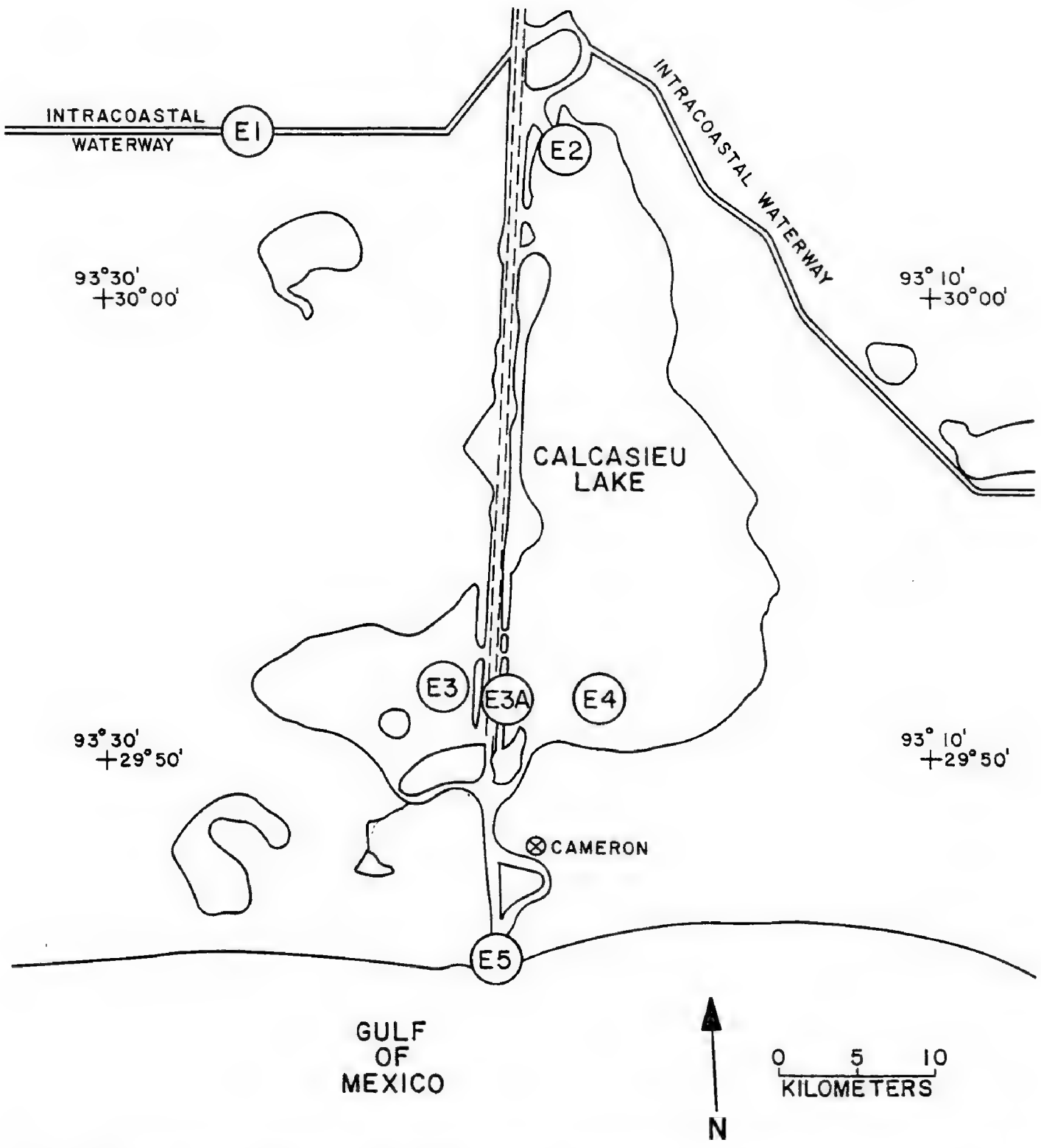

FIG. 1. Station numbers and locations for both pre-storm and post-storm sampling of Calcasieu Lake in southwestern Louisiana.

were from the northeast at 12.3 m/sec, and traces of precipitation were recorded. Tropical Storm Chris moved inland at dawn on September 11. The storm center passed just west of Cameron, Louisiana, and wind speeds up to 30 m/sec from the northwest and 150–200 mm of rainfall were recorded at the National Weather Service office in Lake Charles, Louisiana. Tides were reported to be 1.8 meters above normal. Post-storm sampling was conducted on September 13 when peak winds were from the south at 11.7 m/sec, and no precipitation was recorded.

Physical data for the north to south transect of the lake (E2, E3A, E5) were compared before and after the storm. Salinity (Fig. 2) had decreased at all

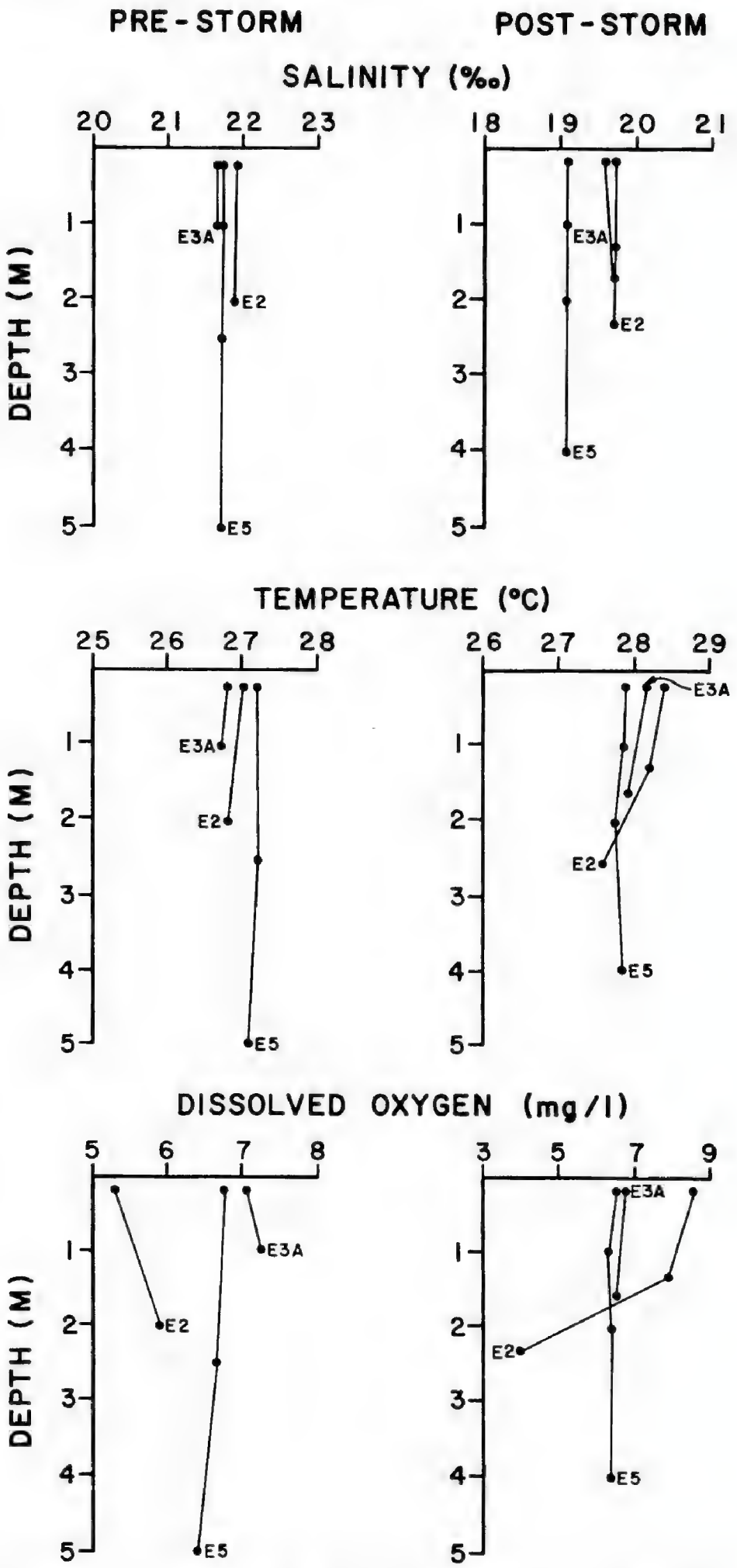

FIG. 2. Pre-storm and post-storm salinity ($\times 10^{-3}$), temperature (°C) and dissolved oxygen (mg/L) profiles for the north–south transect of Calcasieu Lake. Deepest measurement is bottom depth at sampled location.

three stations after the storm and was lowest at the mouth of the estuary. Water temperatures (Fig. 2) had increased at all three stations after the storm, and thermal stratification was evident at the north end of the estuary (station E2). Dissolved oxygen (Fig. 2) had decreased near the bottom at E2 after the storm.

A comparison of pre-storm and post-storm physical data along the east-west transect (E4, E3A, E3) also indicated decreased salinity and increased temperatures (Fig. 3) across the estuary after the storm. Salinity at the channel station (E3A) was lower than that at the nearby shallow stations. Dissolved oxygen in West Cove (station E3) had increased at the surface but had decreased near the bottom after the storm (Fig. 3).

ICHTHYOPLANKTON

The ichthyoplankton was dominated by larval and postlarval Sciaenidae and *Anchoa* spp. In addition to significant ($P < 0.05$) variance among stations for both taxa, two-way ANOVA indicated significant ($P < 0.05$) changes in abundance of sciaenids and anchovies between sampling periods. Student-Newman-Keuls (SNK) analyses indicated that mean abundances of sciaenids were significantly ($P < 0.05$) higher at channel stations E5 and E3A before the storm than afterwards; however, SNK analysis of *Anchoa* spp. abundances was unable to demonstrate either areal or temporal heterogeneity. The Wilcoxon Signed-Rank Test (Table 1) also indicated significantly fewer sciaenids ($P < 0.01$) and anchovies ($P < 0.01$) after the storm.

The dominant taxa of fish eggs were *Anchoa mitchilli* and unidentified sciaenids. Abundances of *A. mitchilli* eggs (Fig. 4) decreased in the ship channel (E3A and E5) and increased in the upper estuary (E1 and E2) after the storm; because of these opposing patterns the Wilcoxon test (Table 1) failed to demonstrate significant differences between pre-storm and post-storm abundances. Fewer scianeid eggs (Fig. 4) were found in the lower estuary (E3, E3A, E4, E5) after the storm, but the data were insufficient to perform a Wilcoxon test.

ZOOPLANKTON

The Wilcoxon test (Table 1) indicated somewhat ($P < 0.1$) fewer decapod zoeae after the storm; this trend appeared to be strongest in the lower estuary (E3, E3A, E4, E5). Before the storm *Pinnixa* sp. and *Neopanope* sp. numerically dominated (22% and 19% respectively) the decapod zoeae assemblage. Lower abundances of *Pinnixa* sp. ($P < 0.1$) and *Neopanope* sp. ($P < 0.05$) resulted from decreased numbers in both the shallow estuary and the ship channel. *Sesarma* sp. occurred in greater numbers ($P < 0.1$) after the storm due to increased abundances at the estuarine stations (E2, E3, E4).

Abundances of total decapod megalopae (Fig. 5) increased after the storm at all stations except E5 in Calcasieu Pass and E1 in the Intracoastal

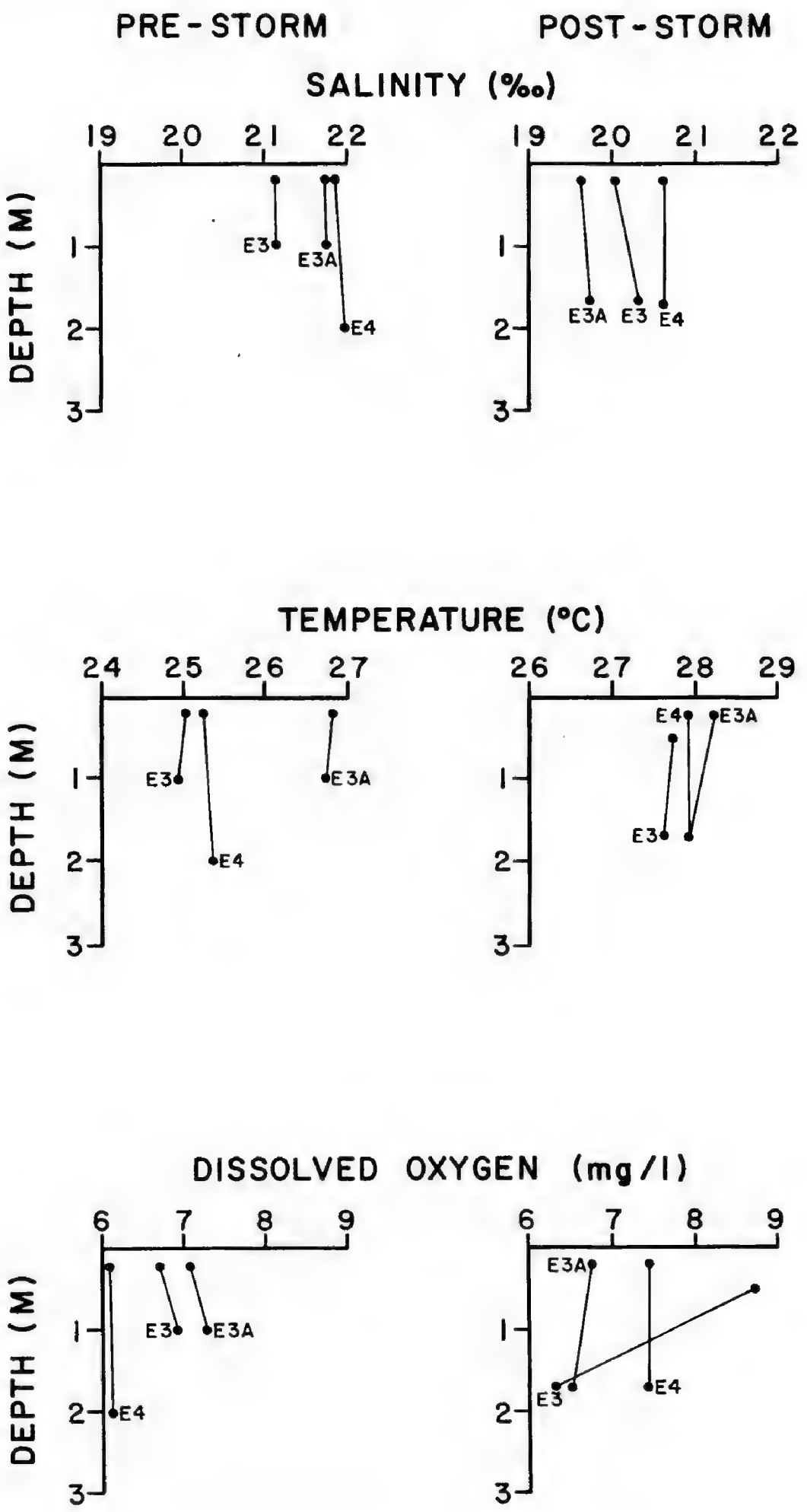

FIG. 3. Pre-storm and post-storm salinity ($\times 10^{-3}$), temperature (°C) and dissolved oxygen (mg/L) profiles for the east–west transect of Calcasieu Lake. Deepest measurement is bottom depth at sampled location.

TABLE 1

Summary of the results of the Wilcoxon Signed Rank Test for selected taxa. *P* values are based upon paired comparisons of pre-storm and post-storm abundances at each station.

TAXA	W	
Anchoa spp.	***	Pre-storm>Post-storm
Sciaenidae	***	Pre>Post
Anchoa mitchilli Eggs		NS
Sciaenidae Eggs		--
Total Decapod Zoeae	*	Pre>Post
Pinnixa sp. Zoeae	*	Pre>Post
Neopanope sp. Zoeae	**	Pre>Post
Sesarma sp. Zoeae	*	Pre<Post
Total Decapod Megalopae		--
Callinectes sp. Megalopae		--
Total Copepods	*	Pre>Post
Acartia tonsa Adults		NS
Acartia tonsa Copepodites		NS

*** $P<0.01$

** $P<0.05$

* $P<0.1$

-- Insufficient data

Waterway; however, the data were insufficient to perform a Wilcoxon test. *Callinectes* sp. (Fig. 5) dominated the megalopal assemblage before and after the storm (94% and 98% respectively) with highest abundances always occurring in Calcasieu Pass. After the storm abundances of *Callinectes* sp. remained stable in the pass but increased further up the ship channel at station E3A.

Copepod abundances decreased in the lower estuary (E3 and E4) and ship channel (E3A and E5) and increased in the upper estuary (E1 and E2) after the storm; however, the Wilcoxon test (Table 1) indicated a decrease ($P < 0.1$) in the overall abundance of total copepods. *Acartia tonsa* dominated the copepod population before and after the storm (40% and 50% respectively Figure 6). Based on the Wilcoxon test neither *A. tonsa* adults nor copepodites demonstrated a significant change in abundance after the storm.

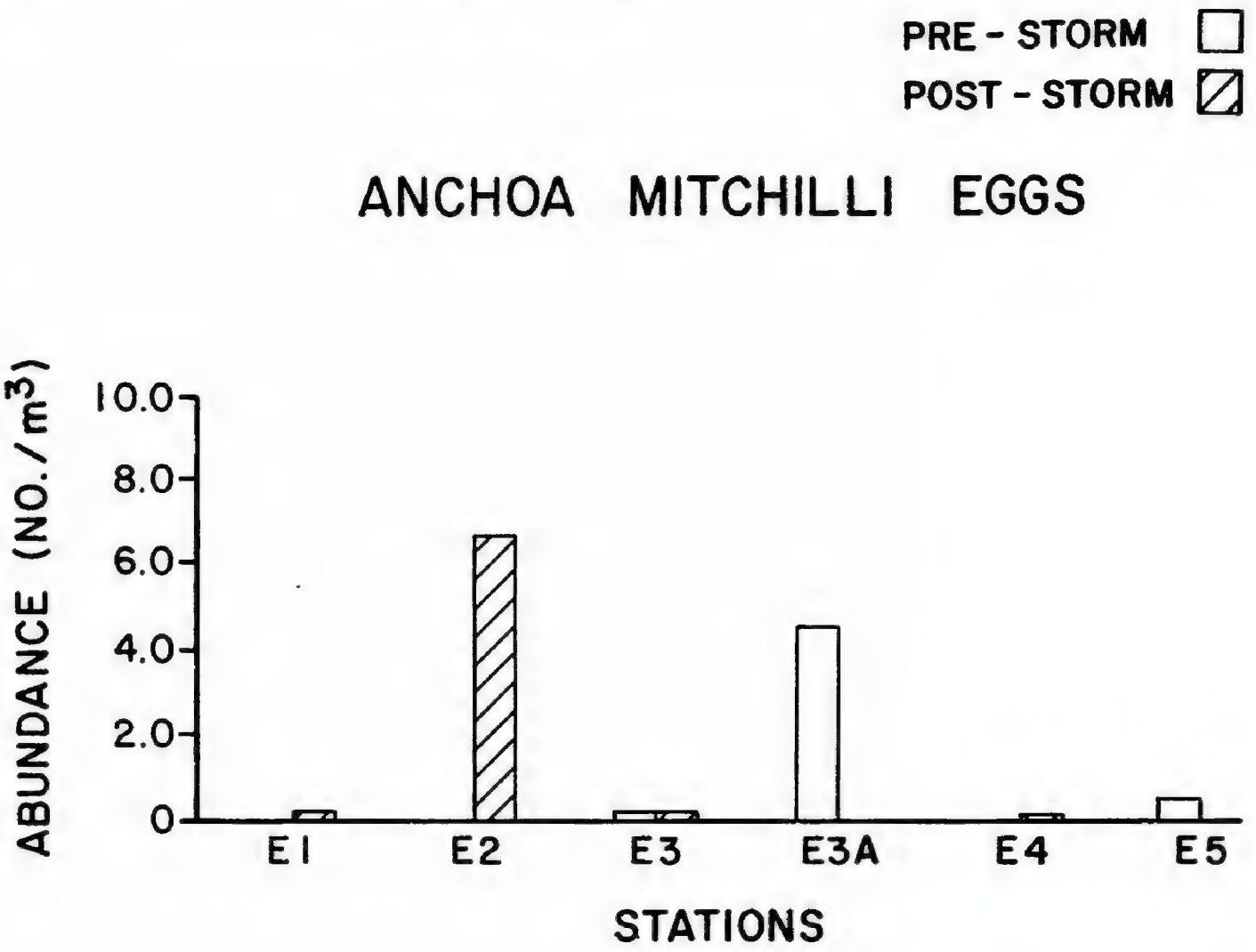

FIG. 4. Abundances of *Anchoa mitchilli* eggs and sciaenid eggs at each station before and after the storm. Each bar represents the density of fish eggs in the first sample of each replicate set.

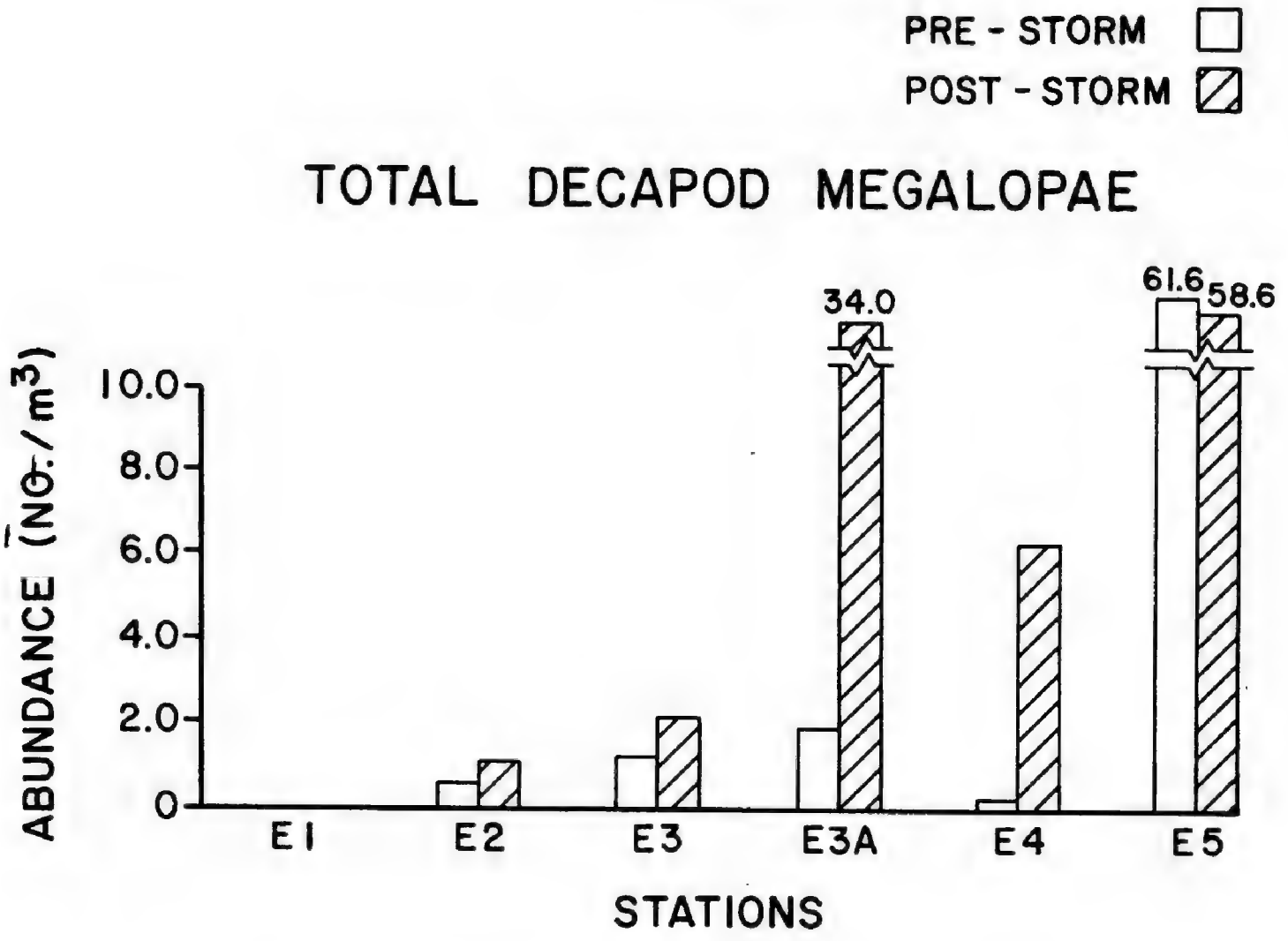

FIG. 5. Abundances of total decapod megalopae and *Callinectes* sp. megalopae before and after the storm. Each bar represents the density of megalopae in the first sample of each replicate set.

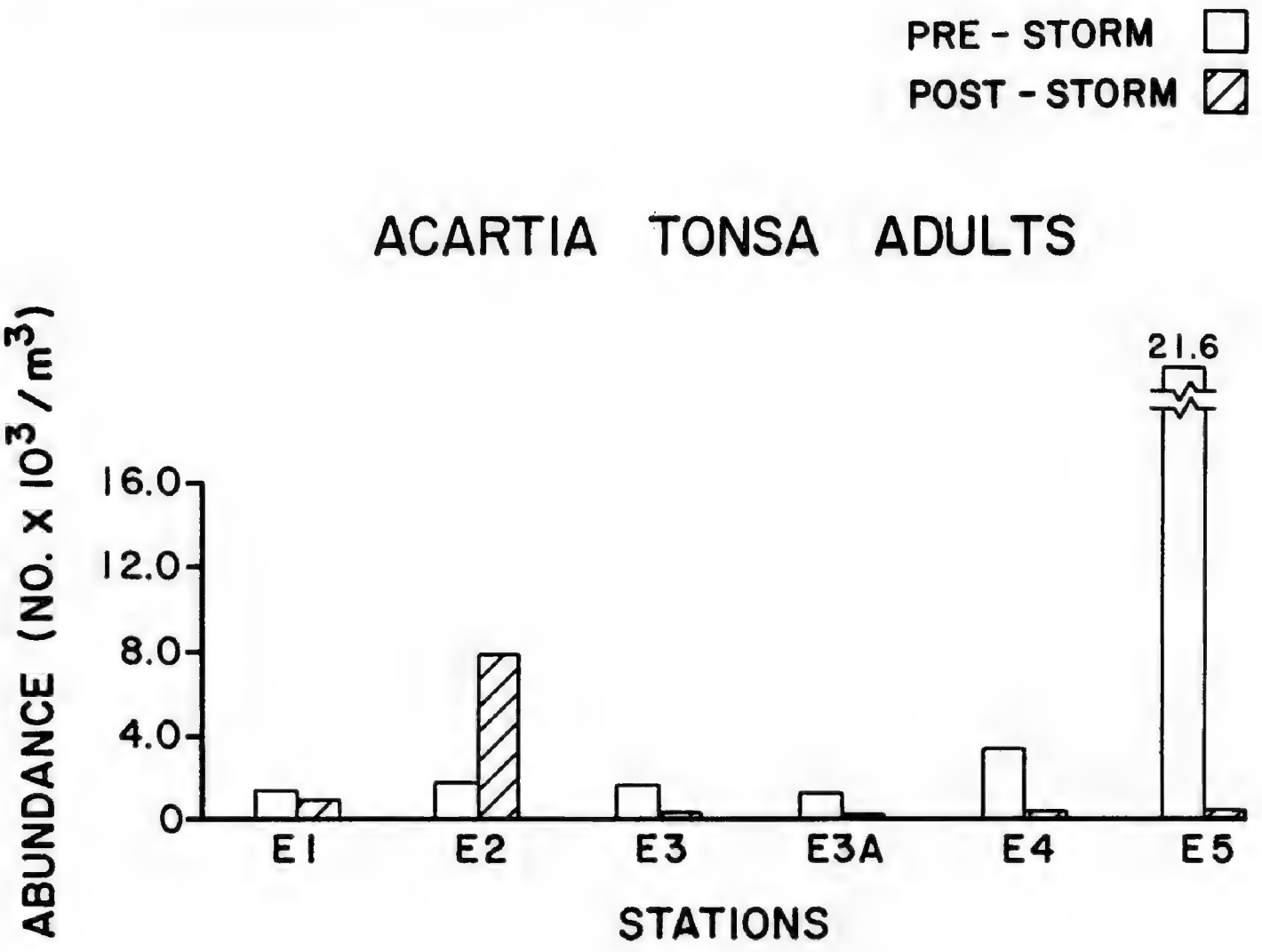

FIG. 6. Abundances of *Acartia tonsa* adults and copepodites before and after the storm. Each bar represents the density of copepods in the first sample of each replicate set.

DISCUSSION AND CONCLUSIONS

The normal hydrography of Calcasieu estuary was temporarily altered by Tropical Storm Chris. After the storm, salinity was lowest at channel stations E5 and E3A. Apparently, a mass of fresh water was moving down the ship channel. An overall increase in water temperature was observed, probably resulting from surface runoff from the storm. Dissolved oxygen was no longer vertically homogeneous but decreased near-bottom at estuarine stations E2 and E3. This change in dissolved oxygen was probably not a result of diel processes such as primary productivity or respiration since sampling was conducted at approximately the same time of day before and after the storm. A likely explanation is that storm runoff from local marshes loaded the estuary with detritus and increased the biological oxygen demand in the system.

A strong trend of decreased abundances was evident for many of the taxa which we examined, and these decreases were most likely storm related. Sciaenid and anchovy larvae and postlarvae occurred in significantly lower numbers after the storm. Sciaenids also underwent significant changes in spatial distribution, decreasing in abundance at stations E5 and E3A, perhaps in response to the freshwater pulse in the lower ship channel. Abundances of *Anchoa mitchilli* eggs and sciaenid eggs decreased somewhat in the lower estuary after the storm; these changes in fish egg abundances cannot be adequately explained by hatching since there was no concurrent increase in larval fish abundances in the lower estuary. Thus, flushing of these planktonic eggs from the estuary seems to be a likely explanation.

The effects of the tropical storm on decapod zoeae appeared to be taxon-specific despite the overall trend of lowered total zoeal abundances after the storm. *Pinnixa* sp. and *Neopanope* sp. abundances were significantly lower after the storm in both the estuary and ship channel, probably due to high winds and freshwater runoff flushing the zoeae out of the estuary. Increased abundances of *Sesarma* sp., particularly at estuarine stations E2, E3, and E4, may be the result of flushing of zoeae from nearby tidal creeks into the estuary.

Post-storm abundances of *Callinectes* sp. megalopae departed from the patterns of decapod zoeae by remaining abundant in the pass and increasing in abundance further up the ship channel. *Callinectes* sp. megalopae are known to concentrate near the mouths of estuaries (Epifanio and Dittel 1982, Sulkin and Van Heukelem 1981) and were most abundant in Calcasieu Pass both before and after the storm.

Post-storm abundances of total copepods were lower than abundances before the storm, particularly in the lower estuary. These planktonic organisms may have been flushed seaward by high winds and increased runoff. The largest decreases in *Acartia tonsa* abundances (adults and copepodites) occurred in the lower estuary and in the ship channel (Fig. 6), but unlike total copepods, the decreases were non-significant. In Chesapeake Bay, Grant *et al.* (1974) and Heinle *et al.* (1974) concluded that *A. tonsa*

was unaffected by Tropical Storm Agnes in 1972; however, their comparisons were made interannually. Monthly comparisons of *A. tonsa* abundances showed little change during floodwater diversion in Louisiana and Mississippi (Hawes and Perry 1978). In Calcasieu Lake the lower abundances of *A. tonsa* adults and copepodites in the lower estuary suggest minimal storm impact due to flushing.

In summary, Tropical Storm Chris produced several short-term changes in Calcasieu Lake. The physical nature of the estuary (*i.e.* salinity, temperature, DO) was altered, with a mass of fresh water evident in the lower ship channel at stations E5 and E3A. Significantly fewer larval and postlarval *Anchoa* spp., larval and postlarval Sciaenidae, total decapod zoeae, *Pinnixa* sp. zoeae, *Neopanope* sp. zoeae and total copepods were found after the storm, and changes in zooplankton distribution among stations appeared to be storm-related. Significantly greater numbers of *Sesarma* sp. zoeae and non-significant changes in *A. tonsa* abundances indicate taxon-specific storm effects rather than a generalized decrease in all zooplankton due to increased runoff or wind-induced flushing.

ACKNOWLEDGMENTS

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ECOLOGICAL SIGNIFICANCE OF SUMMER STORMS IN SHALLOW WATER ESTUARINE SYSTEMS[1,2]

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ABSTRACT

Dissolved oxygen, an integrative community metabolic parameter, was monitored in a shallow, coastal, estuarine water body in Louisiana on days with and without thunderstorms to ascertain the ecological importance of periodic meterorological mixing events. A thunderstorm caused complete overturn of stratified water masses and substantially increased oxygen exchange across the air-water interface. Mixing reaerated bottom waters which stimulated benthic and near-bottom pelagic respiration by a factor of 4. Total community nighttime respiration increased from 8.4 to 15.1 g $0_2 \cdot m^{-2} \cdot d^{-1}$ following storm passage, while community gross production increased 93 percent. A net effect of storm-induced mixing was to decrease the level of heterotrophy in the lake. Analysis of storm data for coastal Louisiana indicates a high frequency of occurrence of summer storms of sufficient magnitude to completely mix shallow estuarine water bodies. Periodic mixing and reaeration of bottom waters may be an important mechanism that increases the habitat value of shallow water bodies to commercially important fishery species.

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INTRODUCTION

Physical processes, such as currents and turbulence, play an extremely important, but poorly understood, role in regulating ecological processes in aquatic systems. Horizontal advection and vertical mixing are critical parameters that partially control such processes as the migration of larval

and juvenile organisms, the replenishment of nutrients in the euphotic zone, and the oxygenation of bottom waters (Mortimer 1942). The interaction of physical and biological processes is widely recognized but rarely quantified.

The objective of this communication is to report the occurrence and ecological significance of summer thunderstorms on thermally stratified, shallow coastal lake systems in Louisiana, USA. In particular, time series measurements of dissolved oxygen and temperature profiles were made in a shallow coastal lake prior to, during and following the passage of an intense thunderstorm. Information is provided concerning the frequency of storms that are of sufficient magnitude to completely overturn lake water columns.

SITE DESCRIPTION

Observations were made at Lake Cataouatche (29°40′N–90°30′W), Louisiana, during June and July 1977, as part of a year-long study of aquatic primary productivity (Hopkinson and Day 1979). Cataouatche is a shallow (1.9 m), brackish water (0–3‰), hypereutrophic lake of 3,700 hectares in Barataria Basin that receives considerable upland and urban rainwater runoff from portions of metropolitan New Orleans.

MATERIALS AND METHODS

Dissolved oxygen concentration was continuously recorded for intervals of at least 24 hrs during June and July 1977 with polarographic electrodes (Martek Instruments Inc., Irvine, California, USA) 20 cm below the lake surface and 30 cm above bottom. The depth profiles of dissolved oxygen and temperature were measured periodically. Community metabolic parameters (gross production and respiration) were calculated using the free water diurnal oxygen technique (Odum and Hoskins 1958). A correction for diffusion was made using the wind speed-percent saturation-effective diffusivity relationships developed by Kanwisher (1963), Kinsey (1978), and Marsh and Smith (1978). Wind speed was measured periodically with a hand-held anemometer and water column transparency was estimated with a secchi disk. Thunderstorm intensity and frequency statisticis were compiled from National Weather Service records collected at New Orleans International Airport (25 km to the north of study site).

RESULTS AND DISCUSSION

In July, dissolved oxygen concentrations were recorded during a calm period without thunderstorm passage (Fig. 1). The surface portion of the water column experienced a substantial diel fluctuation in dissolved oxygen from 13.4 mg O_2/L shortly after mid-day to 5.3 mg O_2/L prior to sunrise. In marked contrast, the range of dissolved oxygen was considerably less in the lower portion of the water column. This pattern of diel oxygen excursion was typical for days without storms during the summer months (Hopkinson and Day 1979). Secchi depths indicated that photosynthesis could not occur in the bottom water (*i.e.* less than 1% of surface light intensity).

In June 1977, observations were conducted during an interval in which there was an intense thunderstorm. The depth profile of dissolved oxygen and temperature at the outset of the monitoring (1200 hrs, 23 June)

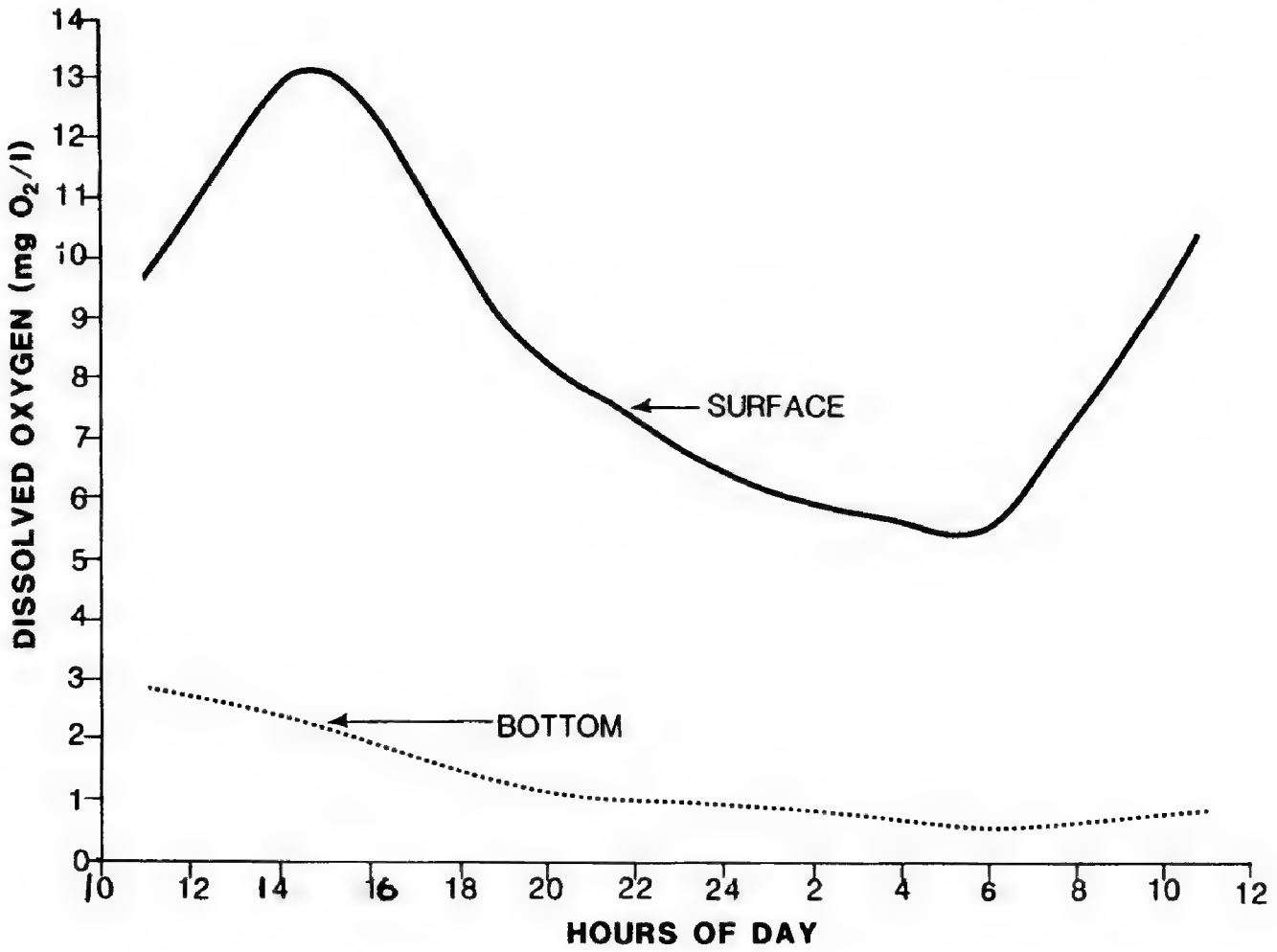

FIG. 1. Diel pattern of dissolved oxygen content in upper and lower water masses in Lake Cataouatche on a day without a thunderstorm.

indicated a stable, stratified water column with relatively uniform and high temperatures and oxygen content in the surface layer and lower temperatures and markedly reduced oxygen content in the bottom water (Fig. 2). Until just before 1500 hrs, the time course of dissolved oxygen (Fig. 3) in both surface and bottom waters was similar to that observed in July (Fig. 1). The supersaturated concentrations in the surface waters were the result of high primary productivity brought about by elevated nutrient loading to the lake from upland runoff (Hopkinson and Day 1979, Seaton 1979). Bottom waters had substantially lower oxygen concentrations than the surface waters because of high oxygen demand by the benthos, the absence of light and hence primary production, and insufficient water column mixing.

At about 1445 hrs, 23 June, a thunderstorm entered the area. Sustained wind velocities of 10 m/s were measured (Fig. 3), with higher values during gusts. Waves up to 60 cm in height quickly developed. The duration of the storm was about 45 min and was sufficient to cause a complete overturn of the water column. Surface and bottom oxygen levels rapidly equalized. Through the rest of the day and night dissolved oxygen decreased at similar rates in both surface and bottom waters. Similar oxygen concentrations in surface and bottom waters during the night indicated that the water column remained well mixed. However, after dawn, surface dissolved oxygen concentrations increased to levels measured the previous day, while bottom oxygen levels showed little change.

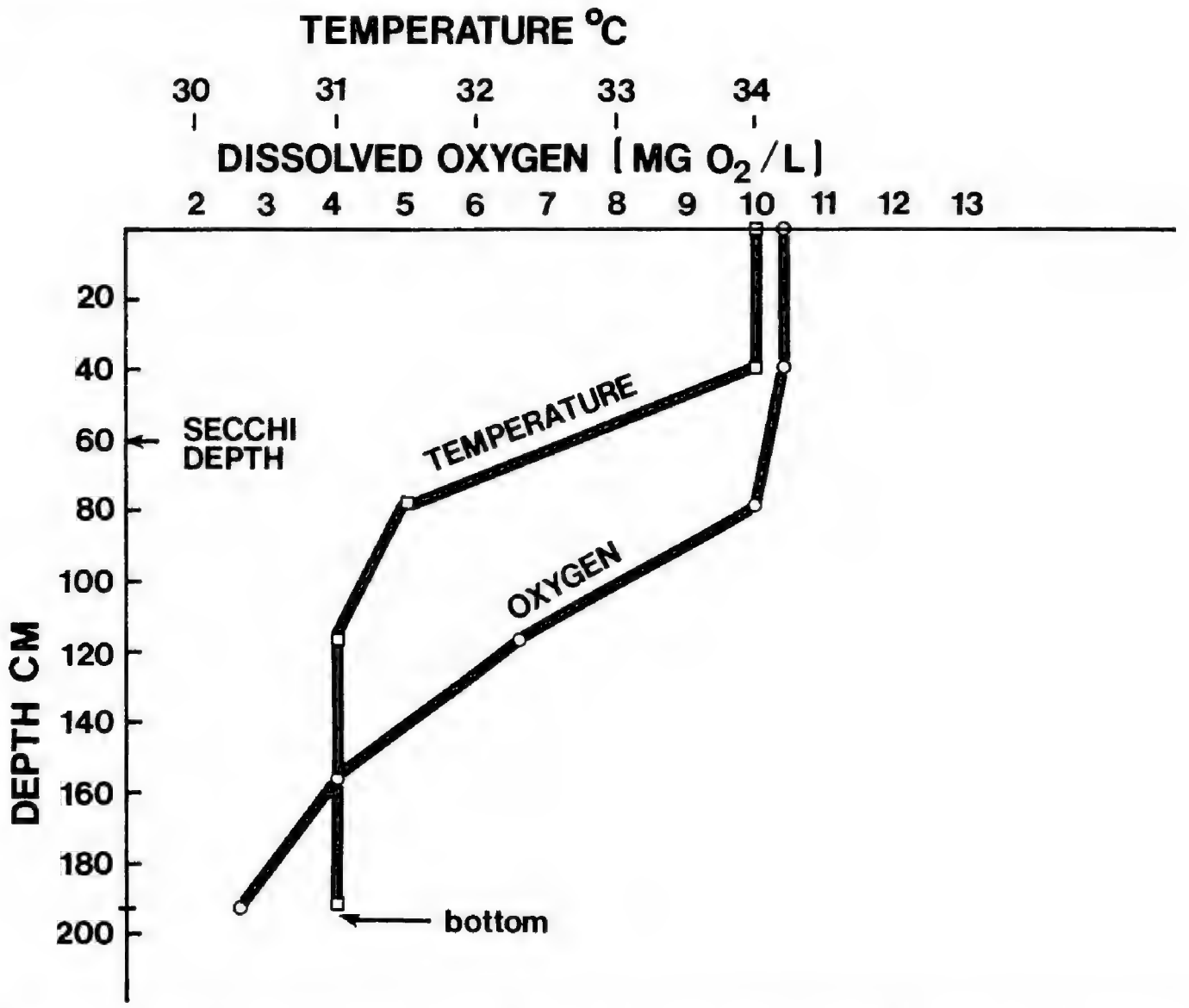

FIG. 2. Temperature-dissolved oxygen profile in Lake Cataouatche 2 hours prior to storm passage.

Thunderstorm passage caused the diel pattern of oxygen concentration to change substantially from that observed on calm days. In the bottom water mass, there was relatively little diel change in dissolved oxygen during calm periods. Immediately following storm mixing of the water column, however, dissolved oxygen changed substantially in the bottom water mass. Whereas the average rate of change in dissolved oxygen was less than -0.1 mg $O_2 \cdot L^{-1} \cdot hr^{-1}$ during calm days, it increased to -0.34 mg $O_2 \cdot L^{-1} \cdot hr^{-1}$ upon mixing. Thunderstorm-induced mixing also had a substantial effect on the surface water oxygen content. On stormless days, as in July, dissolved oxygen decreased slowly during the later afternoon hours. The mixing event, however, caused an immediate sharp decline in surface oxygen content during the same hours.

Overall community metabolic rates in the lake system were substantially altered by the storm. Nighttime respiration was 8.4 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in the absence of a storm and increased to 15.1 g $O_2 \cdot m^{-2} \cdot d^{-1}$ following the storm. The greatest storm effect was on respiration in the benthos and bottom water (0.8 *vs* 3.1 g $O_2 \cdot m^{-2} \cdot night^{-1}$, without and with storm, respectively). On the calm day in July there was little diel change in dissolved oxygen.

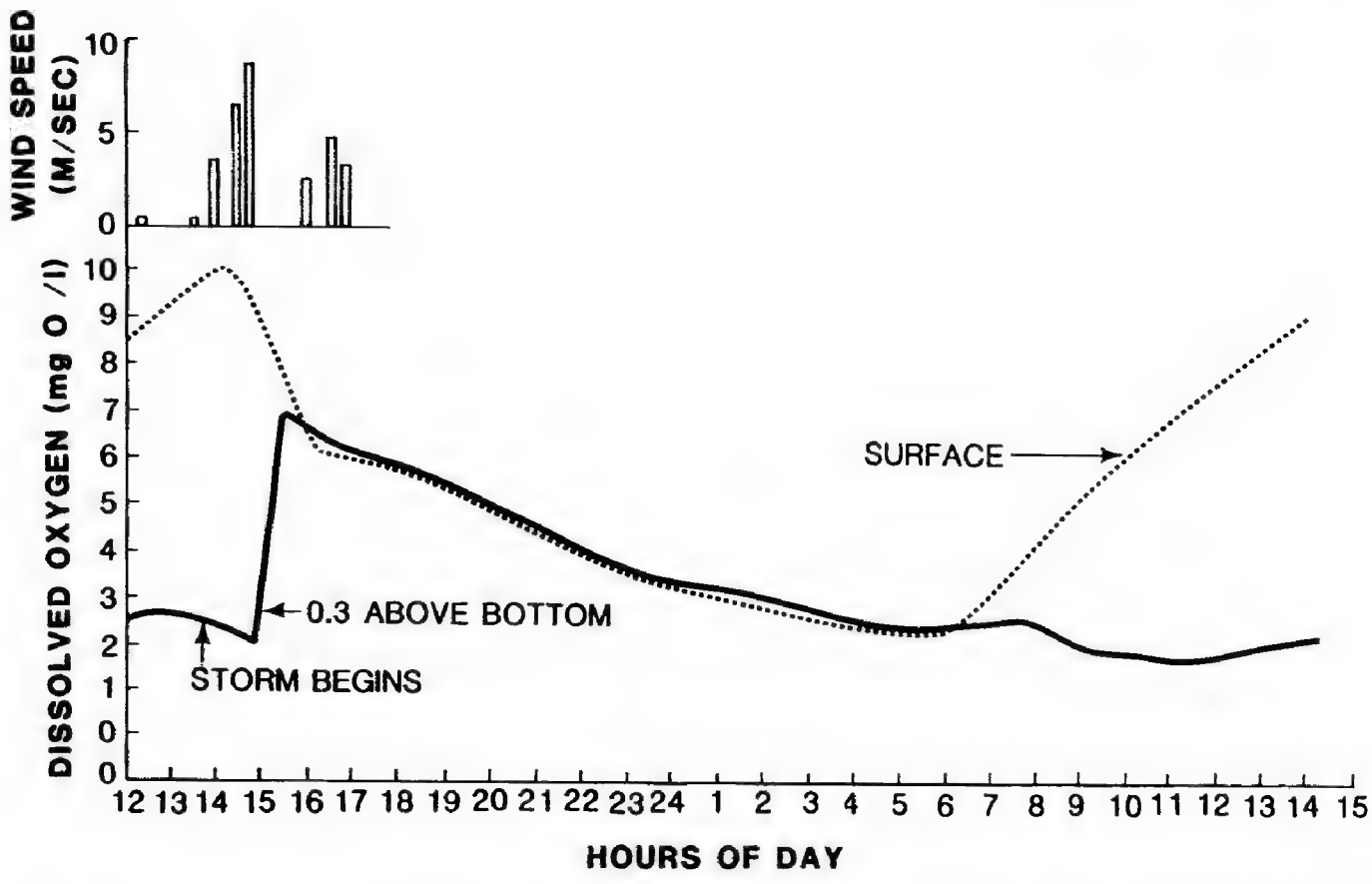

FIG. 3. Concentration of dissolved oxygen in upper and lower water masses in Lake Cataouatche. At 1445 hours, 23 June, an intense thunderstorm passed over the lake, completely mixing it. Bar graph at upper left shows wind speeds measured between 1200 and 1700 hours.

Aerobic benthic and pelagic respiration in the bottom water was probably limited by the slow rate of eddy diffusion of oxygen from the upper water mass. By oxygenating bottom waters the storm stimulated aerobic respiration. There was an even greater increase in the degree of stimulation of gross production. Gross production was 93% higher on the day with a storm (13.7 g O_2 *vs* 7.1 g $O_2 \cdot m^{-2} \cdot d^{-1}$). Not only were the individual metabolic rates stimulated by storm-induced mixing, but the entire autotrophic/heterotrophic balance of the lake was shifted toward neutrality. The primary production to respiration ratio (P/R) was 0.84:1 on the day without storm passage and 0.90:1 on the day of the storm.

Storm-induced mixing in Lake Cataouatche altered oxygen exchange across the air-water interface. Based on the annual imbalance between gross production and respiration of 350 g $O_2 \cdot m^{-2}$ (Hopkinson and Day 1979), we calculate that the net diffusion rate must, on the average, equal 0.96 g $O_2 \cdot m^{-2} \cdot d^{-1}$. After the first few minutes of the storm, the oxygen content of the surface water was lowered from above to below saturation: thus diffusive oxygen flux was directed into the lake rather than out. At the maximum recorded wind speed, the effective diffusivity, K, is in the range of 2.5–3.5 $m^2 \cdot hr^{-1}$ at 100% air saturation deficit (Kanwisher 1963, Marsh and Smith 1978, Kinsey 1978). With a 10% saturation deficit, 25% of the daily diffusion requirement could be met during a storm lasting one hour. These figures indicate that thunderstorm-induced turbulence plays an important role in lake reaeration.

Analysis of storm data for the Cataouatche region indicates a high potential for wind-induced mixing in the shallow water estuarine systems in Louisiana. Thunderstorms in Louisiana occur most frequently during the summer. National Weather service statistics from New Orleans (Fig. 4)

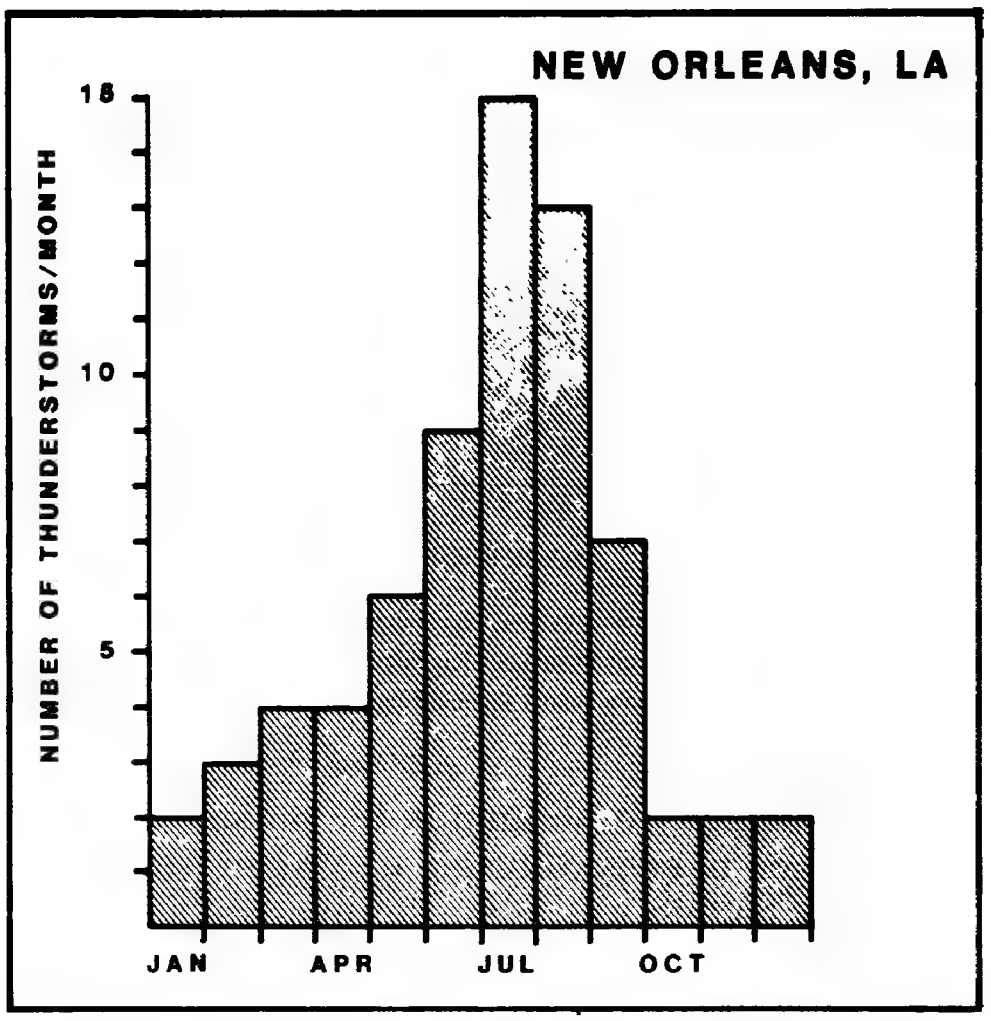

FIG. 4. Thunderstorm frequency statistics from New Orleans International Airport, based on National Weather Service records for a 33-year period.

indicate that July, on the average, has 15 days with thunderstorms and that August has 13. The thunderstorm frequency of occurrence for other months is significantly lower, particularly from October through April. Thunderstorms are characterized by strong ground wind speeds and quickly changing wind directions. Locally, the typical thunderstorm has a duration on the order of an hour and is associated by strong wind gusts, at times exceeding 30 m/sec. As June, July and August are the months of the year when stable thermal lake stratification is strongest and most frequent, it is apparent that the winds associated with thunderstorms can be important mechanisms whereby wetland lakes can be overturned.

We estimate that mixing in Lake Cataouatche commenced when wind speeds attained 5 m/s. From analysis of wind statistics (Fig. 3) recorded by the National Weather Service at New Orleans International Airport, we determined that during the peak thunderstorm season from June through August along the Louisiana coast (Fig. 4), wind speeds of 5 m/s or greater

occur on 34% of the days (Fig. 5). Thus, on the average, the lake mixes completely every third day during the summer.

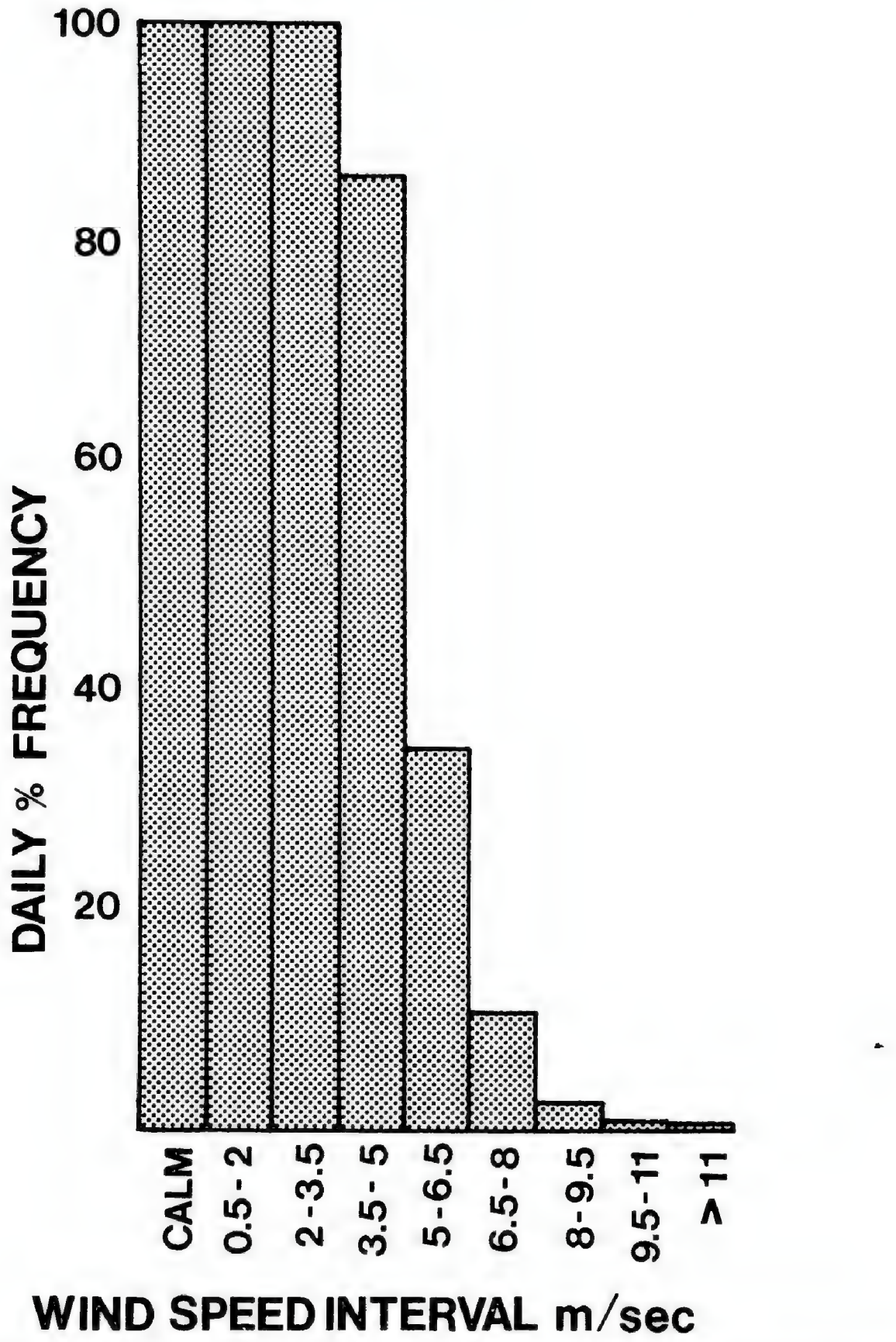

FIG. 5. Daily frequency of occurrence of various wind speeds in coastal Louisiana during the months of June, July, and August, 1975–1979 (Source: NOAA 1975–1979).

These observations show that thunderstorms can strongly affect many physical, chemical, and biological processes in the shallow, coastal waters of

Louisiana. Thunderstorms can completely mix shallow water masses, augment oxygen transfer to the benthos, increase gas diffusion across the air-water interface, stimulate respiration and primary production, and increase the level of autotrophy. The storm-induced augmentation of benthic metabolism can be expected to be coupled with increased nutrient remineralization by the benthos (Nixon 1979). This coupling is probably largely responsible for the positive correlation Nixon found between rates of benthic metabolism and surface primary production.

The ecological importance of thunderstorms can be further appreciated by considering the probable impact of their absence. Day, Hopkinson and Conner (1982) showed that the major source of nutrients sustaining high rates of primary production in Barataria Basin lakes and bays was from the benthos. Without occasional storms, primary production in the upper euphotic zone could be reduced, reflecting the decreased supply of nutrients from the benthos. In the absence of storms, primary production would be limited by nutrient remineralization within the water column, nutrient input from upland runoff, and the slow diffusion of nutrients from bottom waters (Ruttner 1970, Steele 1974). With oxygen supply to the hypolimnion reduced, oxygen demand created by organic matter settling from the surface waters could result in oxygen depletion (Hutchinson 1957). This could lead to a buildup of organic matter on the bottom, and increased frequency of anoxic conditions. However, as primary production would also be reduced, the fallout of organic matter to the benthos would similarly decrease. The extent of anoxia would therefore be controlled by a balance between lower rates of primary production and benthic and pelagic respiration. As our observations showed a decreased level of heterotrophy in the short-run, we might expect periods of anoxia to increase in the absence of storm mixing.

The periodic mixing and reaeration of lower water masses brought about by summer thunderstorms may be an important mechanism that increases the habitat value of shallow water bodies to commercially important fishery species. Chambers (1979), Rogers (1979), Smith (1979), and Day *et al.* (1982) documented the importance of these shallow fresh and brackish water lakes as prime nursery areas for many migratory fish species. They noted that environmental stresses on the fishes were high and increasing, and that anoxic conditions occasionally brought about fish kills. By aerating bottom water, storms may make it possible for organisms, sensitive to low oxygen conditions, to utilize these areas. Without the storms the value of the water bodies as nursery areas might diminish significantly.

The regulatory effects that thunderstorms appear to have on the ecology of Lake Cataouatche probably exist in other shallow water estuarine systems as well. Rigorous investigations are needed to more fully determine the manner and extent to which storms alter primary productivity, respiration, nutrient regeneration and the nursery value of these systems.

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THE EFFECTS OF HYPOXIA AND BRINE ON RECOLONIZATION BY MACROBENTHOS OFF CAMERON, LOUISIANA (USA)

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ABSTRACT

Screened defaunated sediment containers were placed on racks 100 m downcurrent and 10 km upcurrent of a Department of Energy brine diffuser located in the nearshore Gulf of Mexico 20 km southwest of Cameron, Louisiana. Samples were periodically collected from both racks over a period of 14 weeks to assess recolonization by the macrobenthos.

A disparity in dissolved oxygen levels of the two sites led to a disruption of recolonization at one site, and a subsequent dissimilar temporal pattern there. This difference in recolonization of the two sites was apparent in analyses of numerically dominant species and feeding groups until the tenth week of the study. By the end of the study, however, differences between diffuser and control sites were limited to earliest colonizers (surface deposit feeders and suspension feeders) and carnivores, and did not occur in the subsurface deposit feeders that colonized after the severe hypoxia.

High densities of juveniles among the early colonists suggested that initial colonization was primarily established by larval settlement rather than adult immigration. Community structure in the containers, like that of the natural community, was dominated by opportunistic species. Densities of these dominants equalled and exceeded the natural community in only 4–6 weeks at one site, but a similar response was delayed an additional 2 weeks by hypoxia at the other site.

Examination of the feeding biology of recolonizing species at the two sites indicated earliest colonization, and subsequent domination, by surface deposit feeders and filter feeders. Comparable densities of carnivores and subsurface deposit feeders lagged filter feeders by several weeks, and never reached abundances of surface deposit feeders.

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INTRODUCTION

Studies on recolonization of defaunated sediments over the past few years have contributed considerably to our knowledge of marine soft bottom

communities. Many of these studies concentrated on macrobenthic communities following catastrophic events such as oil spills (Jacobs 1980; Sanders, Grassle, Hampson, Morse, Garner-Price and Jones 1980), storms (Boesch, Diaz and Virnstein 1976), red tides (Dauer and Simon 1976) and hypoxia (Rosenberg 1977, 1980; Pearson and Rosenberg 1978; Santos and Bloom 1980; Santos and Simon 1980a; Dauer 1984). Similar studies included the use of sediment boxes and cages as manipulative recolonization experiments (*e.g.* Woodin 1974; McCall 1977; Virnstein 1977, 1978, 1979; Young and Young 1977, 1978; Hulberg and Oliver 1980; Santos and Simon 1980b). The majority of the manipulative experiments concerned natural disturbances of benthic communities, such as predation, occasional bioturbation, or annual defaunation.

We used the experience gained by these experiments in the design and execution of a study on the effects of brine, concentrated salt water discharged from the leaching of a salt dome for oil storage, on the macrobenthos off southwestern Louisiana. From our ongoing research (Weston and Gaston 1982; Gaston and Weston 1983) we knew that hypoxia during the previous summer (1981) killed many benthic species in the natural community (Gaston 1985). Based on other observations of hypoxia along the northern Gulf of Mexico (*e.g.* Fotheringham and Weissberg 1979; Harper, McKinney, Salzer and Case 1981; Stuntz, Leming, Baxter and Barazotto 1982; Boesch 1983; Pavela, Ross and Chittenden 1983), we believed that hypoxia was probably an annual event in the study area. The purpose of the study, therefore, was twofold: 1) to determine whether recolonizing species (both juveniles and adults) could survive in areas affected by the brine plume, and 2) to determine the effects of hypoxia on recolonizing species within the plume and at a site outside the plume. We assumed that hypoxia would affect both areas concurrently; therefore, we would be able to compare the sites with regard to brine effects, and determine whether hypoxia affected juveniles and adults in the containers as it had affected established populations in the natural community. Populations of most species in the natural community were severely reduced by hypoxia. Others, such as the polychaete *Magelona cf. phyllisae*, were not as adversely affected (Gaston 1985).

MATERIALS AND METHODS

The study centered around a Department of Energy Strategic Petroleum Reserve brine diffuser located 20 km southwest of Cameron, Louisiana (Fig. 1). Brine (approximately 250‰) was pumped from the West Hackberry storage site near Hackberry, Louisiana to the offshore study area at a rate of approximately 79.5 million liters per day. The brine was generally comparable to seawater in ionic ratios, except for slightly higher calcium and slightly lower magnesium concentrations (Jeffrey, Murray, Slowey, Beck, Webre and Grout 1983). Recolonization containers filled with defaunated sediment collected from the control site were placed in areas inside and outside of the brine plume in late May, 1982. The site outside the brine plume (control site, station M20) was located 10 km west of the brine diffuser and was known to be free of brine effects (Gaston and Weston 1983). The site inside the brine plume (diffuser site, station M10A) was 100 m west of the center of the brine diffuser in an area of comparable sediments

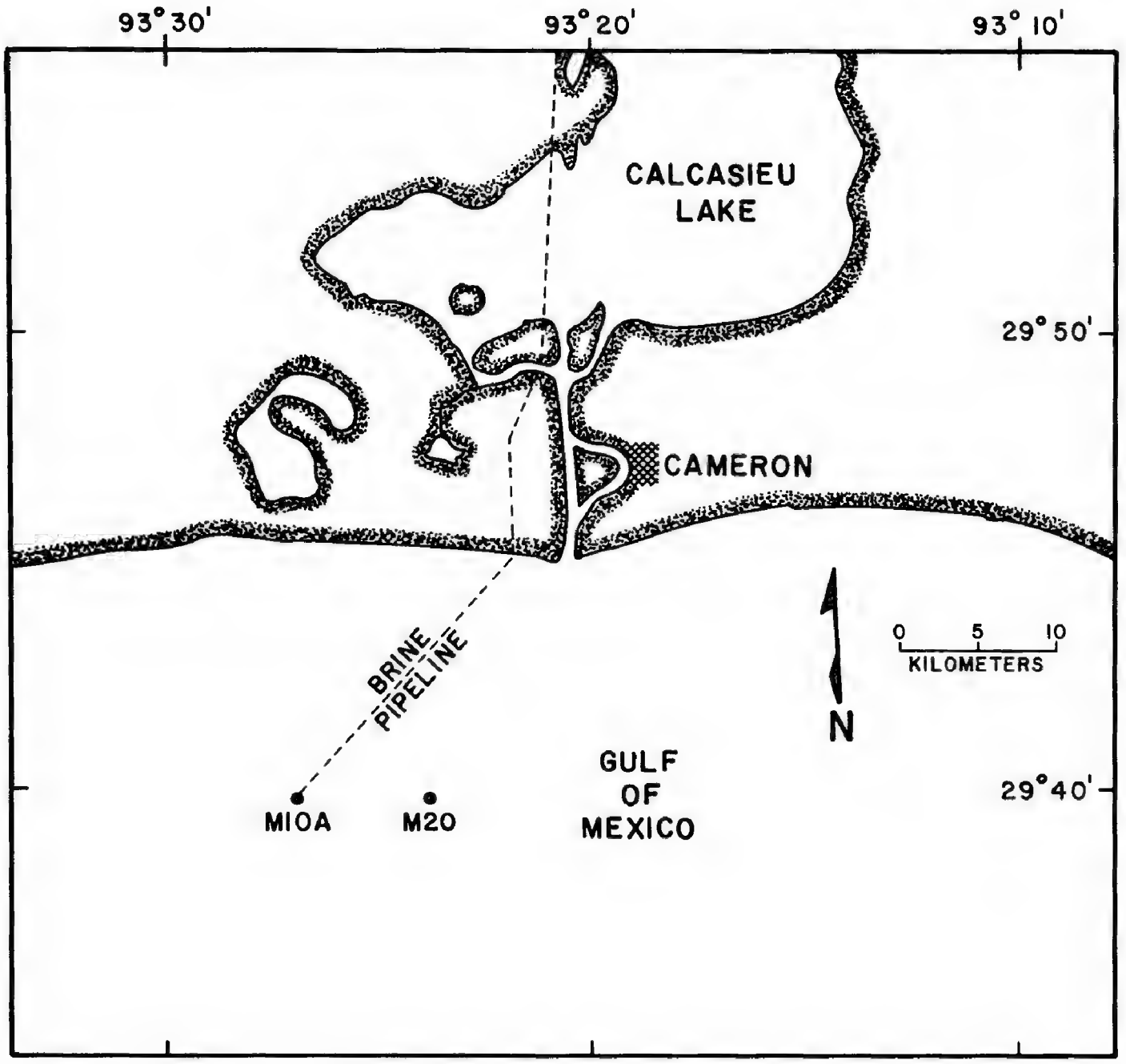

FIG. 1. Study area in the Gulf of Mexico off southwestern Louisiana indicating the two sites (stations M10A and M20) used for the recolonization experiment.

and macrofauna to station M20 (Gaston and Weston 1983). Before the sediment was placed in the containers it was put in plastic-lined drums and allowed to become anoxic over a 7-day period. Each container was then filled within 2 cm of the top with anoxic sediment and frozen at −15°C for 14 days to assure that it was azoic before deployment. Salinity over the bottom of the diffuser site was generally 3–8‰ above ambient due to brine discharge (Gaston and Weston 1983). Both sites were located in 10 m of water.

The containers used for the study were round plastic buckets, 30 cm (diameter) by 20.5 cm (deep). Each container was fitted with a 7 mm mesh plastic predator exclusion screen. This screen was designed to prevent demersal fish and megabenthic species (*e.g.* adult crabs and shrimp) from using the containers as a refuge, and thus disrupting the sediments. Reise (1977) demonstrated that mesh sizes less than 5 mm led to increased sediment deposition. In many studies (reviewed by Arntz 1977 and Virnstein 1978), comparisons between cages and the natural community were confounded because of problems with increased sediment accumulation in the cages. Therefore, since we used screens, we designed the study as a comparison between screened containers at the diffuser site and screened containers at the control site.

Stainless steel platforms held the recolonization containers in place just above the sediment-water interface. These were 1.2 m by 2.4 m expanded steel tables with legs that were driven into

the sediment for stability. Similar platforms were located at each site. In order to prevent sediment scour of the containers, and to minimize the effects of handling by the SCUBA divers, a lid was secured over each container during deployment and again during retrieval.

We wanted to distinguish recently settled juveniles from adults that immigrated into the containers. This distinction would allow us to compare the two sites by abundance of either group, and perhaps determine the effect of hypoxia and brine on both juveniles and adults. Therefore, we washed samples on both 500-μm and 250-μm sieves. We used the term "juvenile" for specimens of the numerical dominants that were small enough to pass through the 500-μm sieve.

Samples were collected weekly for the first 2 weeks and every 2 weeks thereafter. Three containers were randomly selected from each station on each sampling date. Six core samples (46 mm in diameter and 20 cm deep) were then removed from each container. The remainder of the sediment in the container was then discarded. These samples were preserved in 10% buffered formalin. In the laboratory the samples were washed through both 250-μm and 500-μm sieves and all species retained were identified to the lowest possible taxonomic level. Physical data including conductivity, temperature, and dissolved oxygen were taken during each sampling with a Hydrolab Series 8000 instrument package backed up with iodometric determination of dissolved oxygen (Standard Methods 1980). The study continued for 14 weeks until a tropical storm disrupted the containers in September. Statistical analyses included comparison of sites by multiway analysis of variance (MANOVA), and comparisons of species groups by Mann-Whitney U-test (Sokal and Rohl 1981).

It has always been difficult for ecologists to quantify actual environmental damage to benthic communities affected by anthropogenic or natural disturbances. One way to assess such disturbances is to determine effects on the food web, but so little information has been available on feeding of soft bottom continental shelf benthos that food web analyses have usually been impossible. Therefore, community analyses have often ended with comparisons of dominant species at control and experimental sites. Feeding observations in this study and recent publications on feeding of Polychaeta (Fauchald and Jumars 1979; Gaston 1983), however, allowed us to assign most species of macrobenthos to feeding groups (Table 1). These data led to the use of virtually all species in the analyses, whereas previous studies were usually limited to numerical dominants. This classification allowed us to examine the results in terms of feeding groups. We used the feeding biology classifications proposed by Jumars and Fauchald (1977).

RESULTS

In early June, 1982 the bottom water of both sites became hypoxic, but the hypoxia was most severe at station M20, where dissolved oxygen (D.O.) levels were nearly 0 mg/L (Fig. 2). The elevated D.O. levels at station M10A probably resulted from turbulent mixing of the water column by the brine diffuser near that site.

With the beginning of hypoxia in early June, collections at station M20 were almost devoid of macrobenthos, though the first samples collected (after 1 week) at the two sites were similar in both species composition and abundance. Apparently the organisms in the containers had been killed. Diversity indices were used to show the effect on the communities. The use of diversity has fallen in some disfavor among many ecologists in recent years; however, Shannon diversity (Pielou 1966) and its components (species richness and species evenness) proved useful here to illustrate the differences in the two sites soon after the experiment began. All three diversity measurements for station M20 dropped to nearly zero when

TABLE 1

Species collected in recolonizaiton samples. Feeding classification indicated: surface deposit feeder (S); subsurface deposit feeder (B); suspension feeder (F); carnivore (C); herbivore (H); omnivore (O); unknown (U).

PLATYHELMINTHES

Turbellaria

Polycladia sp.A (C)
Polycladia sp.B (C)

NEMERTINEA

Cerebratulus lacteus (C)
Nemertea sp.B (C)
Nemertea sp.D (C)

ANNELIDA

Polychaeta

Lepidasthenia sp.A (C)
Sthenolepis sp.A (C)
Phyllodoce arenae (C)
Gyptis vittata (C)
Gyptis brevipalpa (C)
Podarke obscura (C)
Ancistrosyllis jonesi (C)
Sigambra tentaculata (C)
Sigambra wassi (C)
Sigambra bassi (C)
Nereis lamellosa (S)
Nereis micromma (S)
Glycinde solitaria (C)
Armandia maculata (B)
Capitella capitata (B)
Mediomastus californiensis (B)
Aricidea cf. *alisdairi* (S)
Polydora ligni (S,F)
Polydora socialis (S,F)
Prionospio cirrifera (S,F)
Paraprionospio pinnata (S,F)
Spiophanes missionensis (S,F)
Spiochaetopterus oculatus (F)
Diopatra cuprea (H)
Ninoe sp.A (B)
Lumbrinerides sp.A (B)
Pseudeurythoe paucibranchiata (C)
Magelona cf. *phyllisae* (S)
Cirratulus filiformis (S)
Owenia fusiformis (S,F)
Cistena regalis (B)
Sabellides sp.A (S)
Loimia medusa (S)
Piromis roberti (S)
Megalomma bioculatum (F)

MOLLUSCA

Gastropoda

Teinostoma biscaynense (S)
Vitrinella floridana (S)
Epitonium apiculatum (C)
Crepidula sp. (F)
Polinices sp. (C)
Anachis obesa (C)

Bivalvia

Anadara transversa (F)
Anadara ovalis (F)
Petricola pholadiformis (F)
Tellina versicolor (F)
Macoma tenta (S,F)
Abra aequalis (S)
Mulinia lateralis (F)
Corbula contracta (F)
Cyrtopleura costata (F)

ARTHROPODA

Amphipoda

Corophium sp.B (U)
Melita nitida (U)
Microprotopus sp.A (S)
Parametopella sp.A (S)
Podocerus brasilinesis (S)

Decapoda

Trachypenaeus sp. (O)
Acetes americanus carolinae (O)
Latreutes parvulus (O)
Callianassa sp.B (F)
Upogebia affinis (F)
Portunus gibbesii (O)
Hexapanopeus angustifrons (O)
Neopanope texana (O)
Pinnixa pearsei (O)

SIPUNCULA

Phascolion strombi (F)

PHORONIDA

Phoronis sp.A (F)

ECHINODERMATA

Ophiuroidea

Micropholis atra (S,F)
Hemipholis elongata (S,F)

HEMICHORDATA

Balanoglossus sp.A (U)

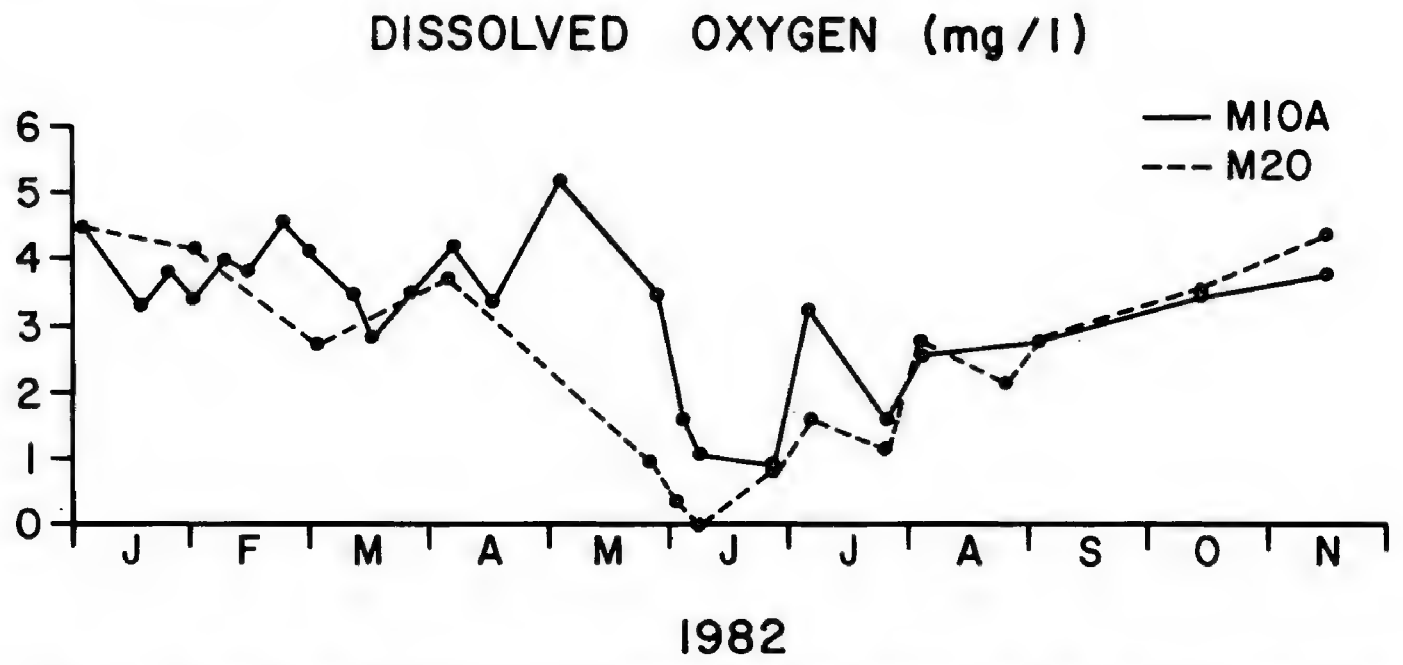

FIG. 2. Temporal variations in bottom water dissolved oxygen during 1982 at the two sites (indicated in Fig. 1).

populations in containers at that site fell in week two of the study (Fig. 3). Diversity values were similar at the two sites throughout the remainder of the study.

Differences in the two sites were also evident in abundances of various species during the early weeks of the study (Fig. 4). Most species that were collected during the first week of sampling at station M20 were absent the second week, then gradually returned thereafter. The result was a 1 to 2 week lag following the hypoxia in recolonization by species at station M20 compared with station M10A. This lag was particularly evident among the numerical dominants. There were significant differences ($P \leq 0.05$) in abundances of most of these species (*e.g. Gyptis brevipalpa*, *Sigambra tentaculata*, *Paraprionospio pinnata*, *Nereis lamellosa*) between the sites soon after hypoxia (weeks 4, 6, and 8). By the end of the 14-week study period, however, collections at both sites were similar in abundances of all but a few of the early dominant species (*e.g. Abra aequalis*, *Sabellides* sp.A, *Piromis roberti*). *A. aequalis*, *S. tentaculata*, and *P. roberti* were never as abundant in containers at M20 as at M10A, perhaps indicating that they were abundantly colonizing only while hypoxia was most severe (early June), and were never as abundant during the remainder of the study.

Differences between juveniles and adults at the two sites are shown in Fig. 5. Although there were never significant differences between collections of adults (those retained on the 500 μm sieve) of *Mediomastus californiensis* at the two sites, significantly more ($P \leq 0.05$) of their juveniles were collected at station M20 during the latter part of the study. This suggestsd that there were more juveniles settling, but fewer juveniles surviving at station M20. Similarly, significantly more juveniles of *Prionospio cirrifera* were collected at station M20, but there were no differences with station M10A in numbers of adults collected. Juveniles of other species among the dominants were also more abundant at station M20 than at station M10A (*e.g. Gyptis brevipalpa*, *Sabellides* sp.A).

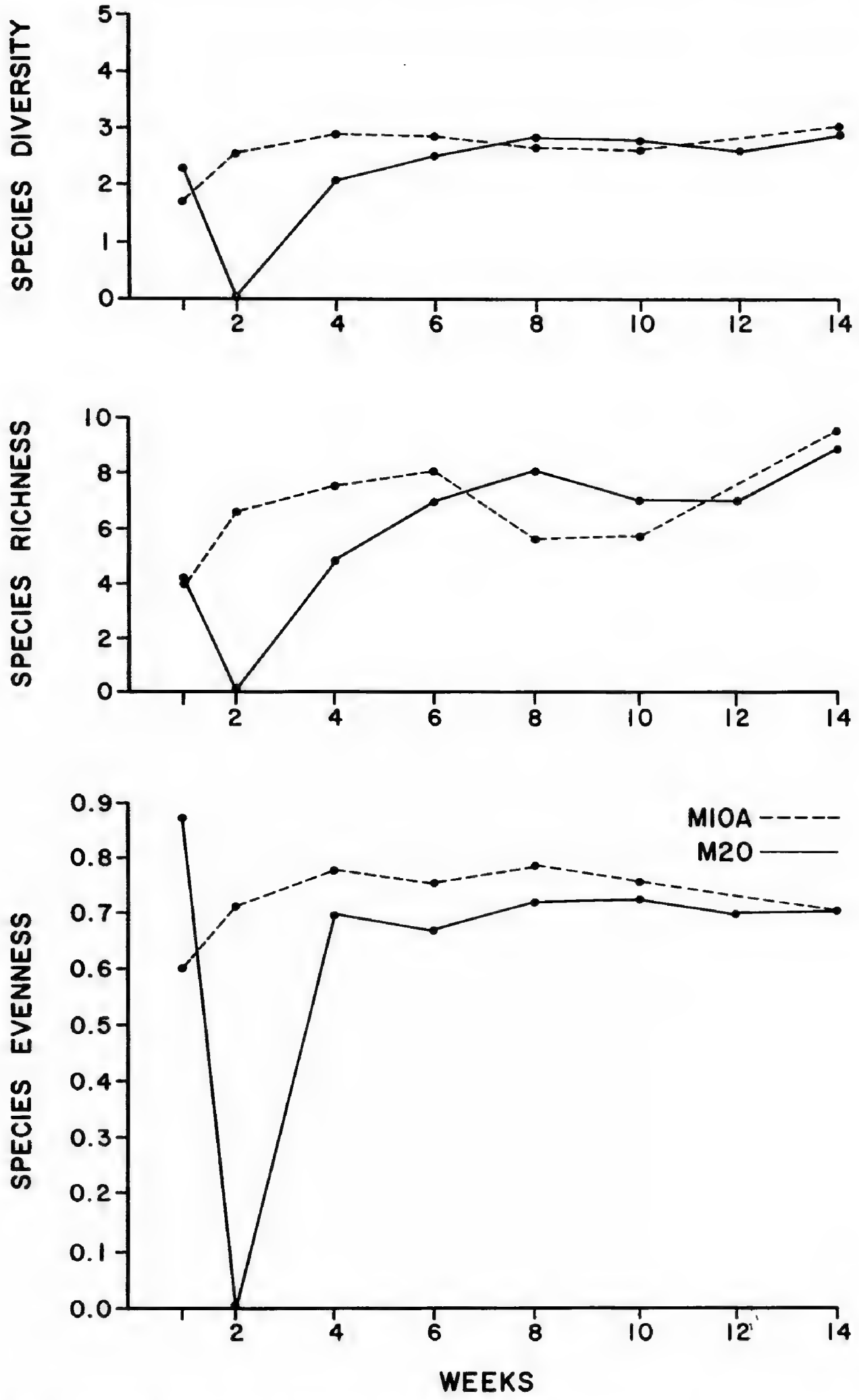

FIG. 3. Temporal variations in species diversity, species richness, and species evenness at the two sites (M10A and M20, indicated in Fig. 1). Sediment containers were deployed at each site in late May, 1982 (week 0 in the figure).

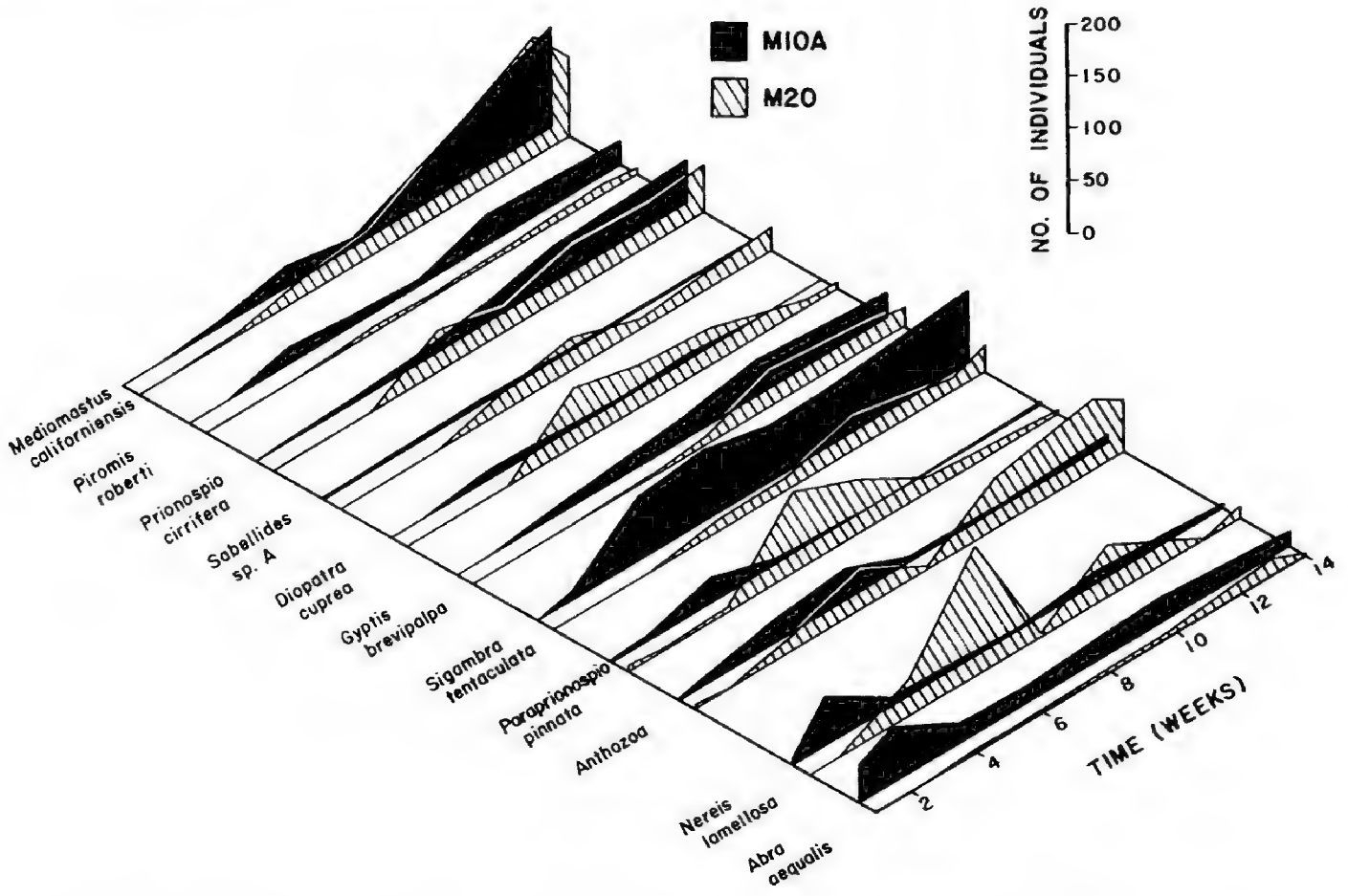

FIG. 4. Densities (individuals per 18 46-mm cores) of numerically dominant taxa at sites M10A (black) and M20 (cross-barred).

Additionally, we wanted to determine whether the differences in abundances of adults between sites were due to fewer recolonizing juveniles or a difference in survival of juveniles and adults. Of the species that were more abundant at station M10A than at station M20 as adults (*e.g. Abra aequalis*, *Sigambra tentaculata*, *Piromis roberti*), none had significantly more juveniles at either site (Fig. 5). Assuming that our sampling of juveniles was adequate, these results suggested that rather than greater numbers of settling larvae causing the discrepancy, the differences resulted from a greater number of juveniles surviving to adult size at station M10A. Conversely, adults of other species, such as *Paraprionospio pinnata*, were more abundant at station M20, even though they too had similar abundances of juveniles at the two sites.

We hypothesized that subsurface deposit feeders (burrowers) would be less affected by disturbances from the water column (*i.e.* brine and hypoxia) than would feeding groups at the sediment-water interface (*i.e.* suspension feeders and surface deposit feeders). Salinity of interstitial water near the brine diffuser (station M10A) was generally about 3‰ lower than overlying water (Gaston and Weston 1983). Additionally, burrowing species, which may regularly encounter low oxygen conditions, should be better adapted to hypoxia than surface-dwelling species. We were unable to address this question, however, because subsurface deposit feeders recolonized later than the other groups (Fig. 6). Such a pattern was evident in the natural

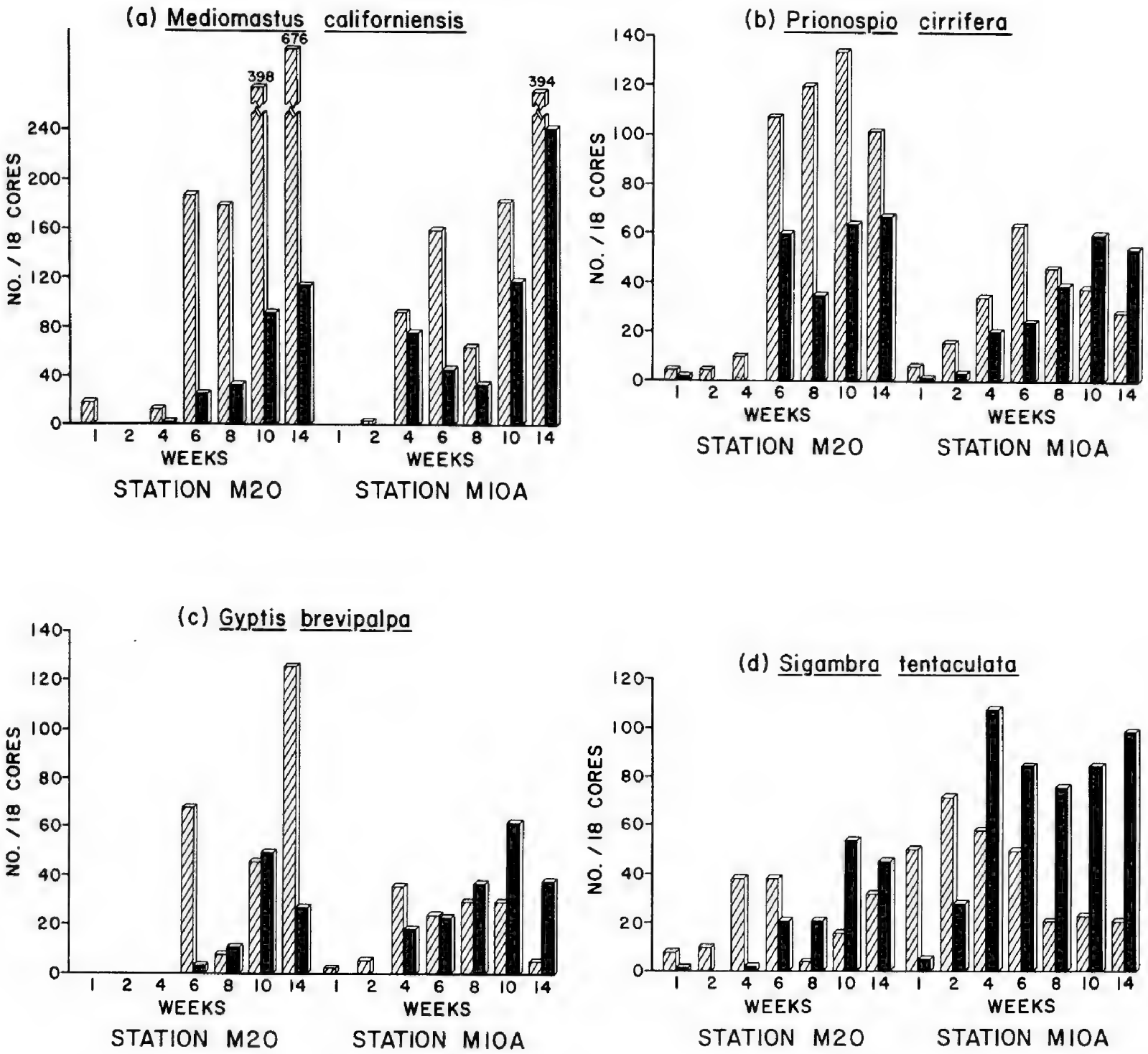

FIG. 5. Densities of four selected species collected by 46-mm diameter cores from experimental containers at the two sites (indicated in Fig. 1). Total juveniles (those retained on a 250-μm sieve) are represented by striped bars. Black bars are adults (retained on 500-μm sieve).

community (Gaston 1985). We found no significant differences in abundances of recolonizing subsurface deposit feeders at the two sites, evidence that brine had no significant effect on subsurface deposit-feeding species as a group.

The earliest colonizers in the containers at the sites were surface deposit feeders and suspension feeders (Fig. 6). Like subsurface deposit feeders, carnivores colonized later. There were significantly more ($P \leq 0.05$) carnivores at station M10A than at station M20 until week 10 of the study. Comparable numbers of carnivores were collected at the two sites thereafter.

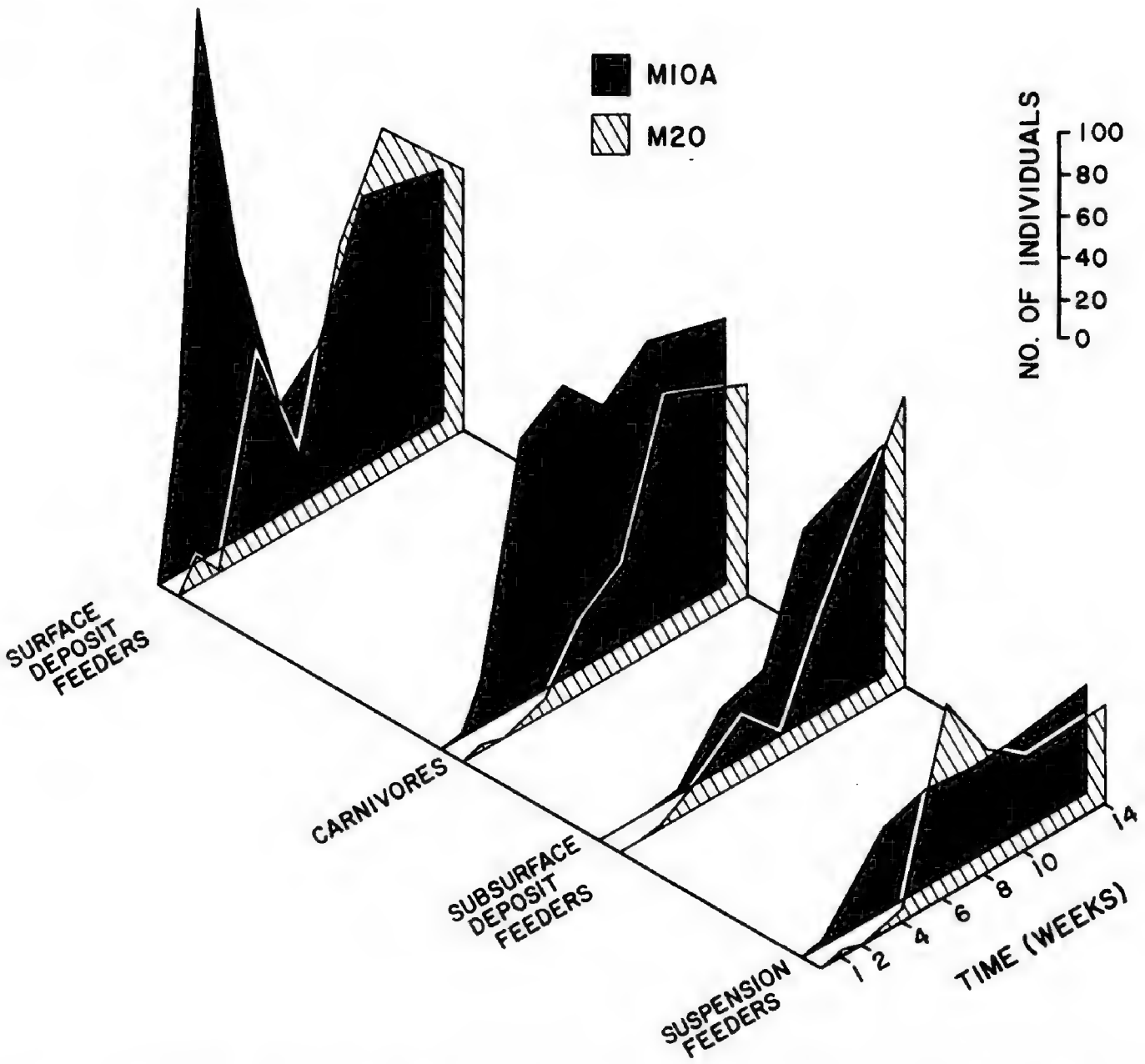

FIG. 6. Densities of four feeding groups presented by site (indicated in Fig. 1). Numbers represent total individuals of each group collected (in 18 46-mm cores) each week. Species represented in feeding groups are indicated in Table 1.

The lag in recolonization at station M20, which was evident in some numerically dominant species, also occurred in some feeding groups: significantly more ($P \leq 0.05$) surface deposit feeders and suspension feeders were collected at station M10A during the early weeks of the study. There were no significant differences between sites in any of the feeding groups after week 10. In short, differences between diffuser and control sites were limited to earliest colonizers (surface deposit feeders and suspension feeders) and carnivores, and did not occur in the subsurface deposit feeders that colonized after the severe hypoxia of early June.

DISCUSSION

This study was designed to determine the effects of brine discharge and hypoxia as separate factors; however, the experimental plan was somewhat

compromised by the early June disparity in dissolved oxygen levels at the two sites. As a result, station M20 became an experimental site for hypoxia effects and a control site for brine effects. Even considering this problem, and the potential for synergistic effects of the two factors involved, the study was valuable for addressing the original questions posed: what are the effects of brine and hypoxia on recolonizing juveniles and adults?

There were differences in recolonization at the two sites, but most of these differences resulted from the lag in recolonization at station M20. A reduction in the natural populations of macrobenthos (Gaston and Weston 1983) and demersal fish and macrocrustaceans (Ilg, Kirby and Stacy 1983) in the area concurrent with the hypoxia supported our hypothesis that the hypoxia (near anoxia), rather than increased predation, killed most of the early colonizing species at station M20, resulting in the lag in recolonization. Populations of most dominant colonists survived hypoxia (1 mg/L) at station M10A, and quickly recolonized station M20 following near anoxia. As in the natural community of the area (Gaston and Weston 1983), most of the early dominants were polychaetes that showed strong resistance to the hypoxia. Boesch and Rosenberg (1981) observed a similar pattern of resistance to hypoxia in populations of polychaetes off the United States east coast. Such resistance to disturbances indicated that communities in the study area were well adapted (resistant and resilient, *sensu* Boesch and Rosenberg 1981) to surviving annual hypoxia, as suggested by Gaston (1985).

There were predictions that the discharged brine would be catastrophic to benthic communities and larvae suspended in the brine plume (reviewed by Comiskey 1979). This did not appear to be the case. Although there were generally more juveniles collected at station M20 than M10A, adult populations of most numerically dominant species were similar at the two sites by the end of the study.

Although larval settlement is generally accepted as the mode of recolonization for estuarine communities dominated by opportunistic species (Grassle and Grassle 1974; Boesch 1977; Pearson and Rosenberg 1978; Santos and Simon 1980b), recolonization on the inner continental shelf has not been as well studied, and recent investigations (Dauer 1984) suggest that adult immigration may be more important than previously acknowledged. Adult immigration, however, did not appear to be an important mechanism of recolonization in our experiment.

As we expected, populations of macrofauna in the experimental containers substantially differed from populations collected by Gaston and Weston (1983) in the natural community. The density of dominant colonists (*e.g. Mediomastus californiensis*, *Sigambra tentaculata*, *Gyptis brevipalpa*, *Paraprionospio pinnata*, *Nereis lamellosa*) at station M10A equalled and exceeded the natural community in only 4–6 weeks, while densities at station M20 lagged those at M10A by about 2 weeks. McCall's (1977) recolonization experiments at comparable depths (14–15 m) in Long Island Sound took only 10 days to match densities in the natural community. Such elevations of macrofaunal density in caging experiments is well documented in the

literature (Arntz 1977; Reise 1977; Virnstein 1977, 1978; Rhoads, McCall and Yingst 1978; Hulberg and Oliver 1980), and substantiates our reservation in extrapolating from these data to comparisons with the natural community.

Recolonization investigations in deeper, more stable marine habitats (*e.g.* Rosenberg 1972, 1973; Grassle and Grassle 1974) demonstrated that opportunistic species, which dominated early in these studies, were gradually replaced by equilibrium species. This replacement did not occur in our study, nor did it occur in similar investigations in south Florida (Santos and Simon 1980a, 1980b, Dauer 1984). Both the south Florida estuary and the natural community of our study area were dominated by populations of opportunistic species. Thus, we never expected equilibrium species to replace opportunists in the experimental containers.

Our use of feeding groups to describe temporal patterns of succession is a relatively new approach. We wanted more than simple comparisons of dominant species at the two stations. It had been suggested that the differential success of potential colonizing species depends on the spatial and temporal extent of the stress causing the disturbance (Boesch and Rosenberg 1981), and that patterns of colonization at the species level are only marginally predictable, or in some cases stochastic (Santos and Simon 1980a). The basic patterns of colonization appear to be predictable, however. Tube-building, surface deposit feeders dominate early stages and pave the way for further succession in the community (Gallagher, Jumars and Trueblood 1983). We found earliest colonization dominated by suspension feeders and surface deposit feeders at both sites. These species produced tubes and burrows that probably enhanced subsequent colonization by changing the pore water chemistry (Aller 1980; Aller, Yingst and Ullman 1983) and increasing oxygenation to the sediments. We did not find replacement of earliest colonists by other species, however. Many of the early dominants remained throughout the experiment. We found that subsurface deposit feeders generally lagged early colonists by several weeks. With the exception of the polychaete *Sigambra tentaculata*, which settled early in the study at station M10A, carnivores also lagged the early dominants. The most salient feature of our comparisons of the two stations was evident in the feeding group analyses: the sites were similar in all feeding group categories by the end of the study (weeks 10 to 14). The differences which occurred in early June (weeks 2 to 6) appeared to be related to hypoxia. Although hypoxia somewhat confounded our use of station M20 as an ideal control, we concluded that discharged brine had no obvious effects on species combined into feeding groups. We recognize, however, that our experiment was of relatively short duration (14 weeks), and provided little insight into effects related to long-term brine discharge.

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INFLUENCE OF WHITE SHRIMP (*PENAEUS SETIFERUS*) ON BENTHIC METABOLISM AND NUTRIENT FLUX IN A COASTAL MARINE ECOSYSTEM: MEASUREMENTS *IN SITU*

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ABSTRACT

Short-term effects of aggregated adult white shrimp (*Penaeus setiferus*) on net rates of benthic metabolism and nutrient flux were measured *in situ* in the nearshore zone of the Georgia Bight. Including white shrimp as components of the benthic system significantly increased both oxygen consumption and ammonia regeneration, but had no discernible effect on fluxes of nitrate, nitrite, or phosphate. In this nitrogen-limited, heterotrophic system, the presence of aggregated adult penaeids resulted in localized increases in both community metabolism and supply of inorganic nitrogen to phytoplankton. These mobile epibenthic macrofauna may stimulate patches of primary productivity and hence secondary production.

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INTRODUCTION

Small organisms tend to have high metabolic rates. These rates have prompted a number of studies examining the influence of microfauna on various aspects of nutrient storage and flux within the ecosystems they inhabit (*e.g.*; Johannes 1964; Eppley, Ranger, Venric, and Mullin 1973; Pomeroy 1974; Bartell 1981). Larger organisms, which have lower weight-specific rates and tend to be less numerous, have received less attention. Yet several studies show that aggregated macrofauna can significantly affect their immediate environment in at least three ways: 1) as consumers regulating the size or species composition of their food resources (Brooks and Dodson 1965; Hurlbert, Zedler, and Fairbanks 1972; Werner and Hall

1974; Bell and Coull 1978), 2) as direct sources of regenerated organic compounds and remineralized nutrients, which enhance microbial and primary productivity (Welsh 1975; Durbin, Nixon, and Oviatt 1979; Kitchell, O'Neill, Webb, Gallepp, Bartell, Koonce, and Asmus 1979; Montague 1982; Elliot, Casternares, Perlmutter, and Porter 1983), and 3) as mechanical agents affecting nutrient flux through physical disturbance of the system (*e.g.*, bioturbation in aquatic environments; Yingst and Rhoads 1980, Aller 1982). Thus, combined trophic, chemical, and mechanical effects of macrofaunal behavior and physiology might produce significant net effects on systems-level characteristics including patterns of nutrient distribution and flux.

Studies of nutrient flux at the sediment-water interface in aquatic systems usually consider only effects of relatively stationary, small-sized benthic and epibenthic fauna such as polychaete worms (Rhoads, Aller, and Goldhaber 1977; Yingst and Rhoads 1980; Aller 1982). Larger mobile epibenthic animals are excluded, even though high densities of transient macrofauna are characteristic of many marine and freshwater environments. Coastal marine ecosystems, in particular, host large populations of migrant macrofauna (*e.g.*, Weinstein 1979).

We report here results of a study designed to examine the potential importance of a large epibenthic migrant in stimulating or augmenting benthic metabolism and regeneration of nutrients in a relatively well-studied marine system, the nearshore zone of the Georgia Bight (Blanton and Atkinson 1978, Hopkinson and Wetzel 1982).

We selected white shrimp (*Penaeus setiferus*) as an example for two reasons: 1) the species is a very common type of migrant through this system, moving seasonally as large populations of adults from estuaries into nearshore zones (*e.g.*, Harris 1974), and 2) white shrimp are known to aggregate on benthic sediments in locally dense patches (Hildebrand 1954, Lindner and Cook 1970). Adults are large (10–20 cm total length), ammonotelic (Vetter 1983), micro-omnivorous heterotrophs (Williams 1958). These habits potentially affect local, short-term patterns of nutrient flux near the benthic boundary layer through selective feeding, bioturbation, excretion of metabolic by-products, and stimulation of other benthic population metabolism.

We conducted the study *in situ* because we wished to estimate net effects in an intact system. Simply adding rates of oxygen metabolism and nutrient flux from lab studies of shrimp, to benthic-system rates measured *in situ* but excluding shrimp, ignores a multitude of potential interactions between various system components (*e.g.*, Pamatmat and Findley 1983). Ammonia flux, for example, in the presence of shrimp could be affected not only by direct excretion from the shrimp but also by sediment disturbance during feeding and consequent stimulation of micro-organism metabolism. The direct approach was appropriate and possible in this case because rates in the absence of shrimp were well-known from previous studies (Hopkinson and Wetzel 1982).

MATERIALS AND METHODS

We conducted the study during September 1981 in shallow water (3 to 5 m) 1.6 km off the coast of Georgia in the nearshore zone of the Georgia Bight (30°27′1″N, 81°12′10″W). Water chemistry and sediment characteristics of this site are well known, because it is one of several that have been visited repeatedly during an ongoing study of benthic metabolism and benthic nutrient dynamics along a transect across the inner continental shelf (Hopkinson and Wetzel 1982). Waters immediately adjacent to the coast in this region are very turbid. Sediments at the study site are 96% fine sand, 1.5% silt, 1.5% clay (by weight) and contain a modest amount of shell material. Sediment organic carbon content is less than 1.2% of dry weight (Hopkinson and Wetzel 1982). Water temperature and salinity were 25°C and 32‰, respectively.

In situ measurements of benthic oxygen uptake and net fluxes of dissolved nitrogen and phosphorus across the sediment-water interface were made in water enclosed by four opaque, acrylic hemispheres (volume = 47.5 L; benthic surface area enclosed = 0.28 m^2). Circular flanges extended horizontally 15 cm across the sediment from each dome. Vertical flanges encircling the enclosed sediment beneath each dome extended 10 cm below the sediment surface. SCUBA divers carefully placed the domes on the bottom to ensure a minimum of sediment disturbance. Initial measurements were made immediately after all four domes were in place.

Shrimp were introduced into the domes immediately after the initial measurements. Sets of shrimp equivalent to densities of 0, 14, 28 and 54 per m^2 were introduced into the chambers through an oxygen probe portal.

These densities were chosen to bracket the range of possible natural densities. Rulifson (1981) reported that large white shrimp (64–168 cm RL) were found on sandy-mud substrate in densities up to about 12 shrimp m^{-2}; mixed species occurred in densities up to 20 shrimp m^{-2}. These represent spacing of non-migrating shrimp contained overnight within relatively small (2.4 m diameter) tanks. We suspect that feeding or migrating shrimp might be aggregated more densely, similar to fish schools, either to exploit patchily distributed food or as protection from predation. Actual density of migrating penaeid shrimp in natural aggregations has not been determined, but anecdotal reports indicate that white shrimp occur in locally dense swarms (Hildebrand 1954, Linder and Cook 1970). Adult white shrimp with walking legs extended normally are about 5 cm wide and 20 cm long (personal observation). They could occur without overlap in single-layer densities of about 100 individuals m^{-2}. We selected half this density as a hypothetical upper limit.

Opaque 300 ml bottles were filled with bottom water and incubated *in situ* to provide a correction for pelagic activity (Fisher, Carlson, and Barber 1982).

After initial measurements in all domes, dissolved oxygen (D.O.) and nutrients were measured approximately hourly in domes and at experiment termination in bottles. D.O. was measured with Orbisphere polarographic oxygen meters equipped with self-contained stirrers. The water in each dome was mixed thoroughly by the oxygen probe stirrer before each measurement. Samples (60 ml) of well-mixed water for nutrient analyses were taken from each dome by syringe. Replacement water was from the water column. Analytical methodology described by Grasshoff (1976) for nitrate, nitrite, ammonium, and phosphate-P was utilized for fixing samples in the field. Water for other analyses was filtered though pre-washed 1.0 μm filters (Gelman A/E glass fiber), stored on ice in the field, and kept frozen in the laboratory until analyzed.

Adult white shrimp were collected by otter trawl (tows less than 10 minutes; 2.5 cm stretched mesh) from the study area on the evening prior to the experiment. The shrimp were not fed any time after capture. A subsample of adult shrimp was placed immediately into a darkened, aerated chamber flushed continuously with flowing seawater. The shrimp remained in the chamber until just prior to the experiment the following day, when three groups of shrimp were selected, all individuals of nearly identical size (12.4 cm TL; S.E. = 0.4; n = 27). Shrimp were handled only once, for length measurement, and then placed directly into submerged carriers for transport to the domes.

Nutrient concentrations in water within the domes were converted to an areal basis (mass • m^{-2}) by multiplying the ratio of dome volume to benthic surface area (*e.g.*, 1 μg-at N L^{-1} × 47.5 L per dome/0.28 m^{-2} per dome = 172.1 μg-at N m^{-2}). Nutrient and oxygen fluxes were calculated on an areal basis after subtracting pelagic activity and accounting for dome volume and enclosed surface area (Hopkinson and Wetzel 1982).

Mean areal mass over time and fluxes of each nutrient and oxygen were analyzed for effects due to shrimp density. Mean areal masses of ammonium and nitrate+nitrite−N in each dome were compared by standard two-way analysis of variance with domes and sample period as factors. Where overall analysis indicated significant differences between at least one pair of means, individual differences were identified using Newman-Keuls multiple range test (Zar 1974). Significant additivity in the interaction term and lack of replication within cells made it necessary to compare mean concentrations of oxygen and phosphate−P by Page's nonparamteric test for ordered alternatives (Hollander and Wolfe 1973). All analyses of mean concentration excluded the initial pre-shrimp sample and were performed on log-transformed data ($y' = \ln(y)$ or $g' = \ln(y + 1)$) in order to conform to the analysis of variance procedure.

Fluxes of oxygen and nutrients in each dome were calculated by linear least squares regression of concentration versus time (after subtracting pelagic activity) and were compared by analysis of covariance. Regressions for each nutrient included the initial pre-shrimp sample. Where simultaneous covariance analysis of all four regressions for any one nutrient indicated significant difference between at least two regressions, Zar's (1974) methods for comparison of multiple slopes and multiple intercepts were used to identify significantly different pairs. All fluxes except ammonia were calculated from log-transformed data ($y' = \ln(y)$ or $y' = \ln(y + 1.0)$). Rate regressions for ammonia were estimated from untransformed data because plots of transformed and untransformed data showed that transformation destroyed linearity in the original data, and did not alter the variance significantly.

RESULTS

The presence of shrimp significantly affected oxygen metabolism and ammonia regeneration, but had no apparent effect on nitrate+nitrite−N or phosphate−P.

Benthic oxygen metabolism (including shrimp as components of the benthos) was significantly higher in domes containing shrimp than in the control dome ($P < 0.05$; Table 1). Although oxygen metabolism in the dome containing 14 shrimp • m^{-2} was not significantly different from metabolism in the dome containing 28 shrimp • m^{-2} it was clear that rate of oxygen consumption increased with increasing shrimp density (Fig. 1b). Densities of 14 to 28 shrimp • m^{-2} increased system metabolism 50% to 100%; rates at the highest density were about 5 times higher than in the control (Fig. 2b).

Shrimp density also had a profound effect on net rates of ammonium regeneration. Mean concentrations and net flux of ammonium from the benthos into the water column increased with increased shrimp density (Table 1, Figure 1a). Ammonia regeneration more than doubled even at the lowest density of shrimp. Regeneration rate in the presence of 28 shrimp • m^{-2} was over 300% higher than in the control dome. At the highest density, regeneration rate was an order of magnitude greater than in the control (Table 1, Fig. 2a).

Concentrations of phosphate−P and nitrate+nitrite−N varied with time in each dome but variations were independent of shrimp density (Table 1; Figs. 1c, 1d, 2c, 2d).

TABLE 1

Mean nutrient and oxygen masses over time, and their rate of change in treatments with various densities of white shrimp. Rates of change were calculated by regression ($y = ax + b$) of mass versus time where y = mass (μg-at N or P • m^{-2} or mg O_2 • m^{-2}), a = slope (μg-at N or P • m^{-2} • hr^{-1} or mg O_2 • m^{-2} hr^{-1}), x = time and b = intercept. Concentrations are in units of μg-at N or P. Analyses performed with logarithmically transformed data are indicated with (ln). Numbers in parentheses are standard errors. Values connected with an underline were not significantly different ($P > 0.05$). See text for an explanation of statistical analyses. R^2 is the fraction of variation in flux that is accounted for by regression.

Comparison	Shrimp density (#/m^2) 0	14	28	54
Ammonium				
Mean concentration (ln)	5.8(0.1)	6.1(0.1)	6.5(0.1)	7.0(0.1)
Flux: Slope	40(9)	85(9)	143(22)	359(44)
Intercept	208	179	205	193
R^2	0.92	0.85	0.92	0.70
Oxygen				
Mean concentration (ln)	6.7(0.1)	6.5(0.2)	6.4(0.2)	5.4(0.5)
Flux: Slope (ln)	0.10(0.002)	0.16(0.01)	0.19(0.03)	0.52(0.03)
Intercept	7.1	7.0	7.0	7.0
R^2	0.99	0.98	0.95	0.98
Phosphate - P				
Mean concentration (ln)	5.5(0.3)	5.7(0.4)	5.3(0.3)	5.5(0.2)
Flux: Slope (ln)	0.24(0.11)	0.22(0.09)	0.22(0.09)	0.23(0.11)
Intercept	4.6	4.8	4.5	4.6
R^2	0.63	0.38	0.69	0.62
Nitrite plus Nitrate - N				
Mean concentration (ln)	3.4(0.4)	3.2(0.5)	3.3(0.5)	3.1(0.6)
Flux: Slope (ln)	1.0(1)	6.0(4)	2.8(4)	3.7(2)
Intercept	5.7	7.0	14.3	7.7
R^2	0.10	0.30	0.10	0.37

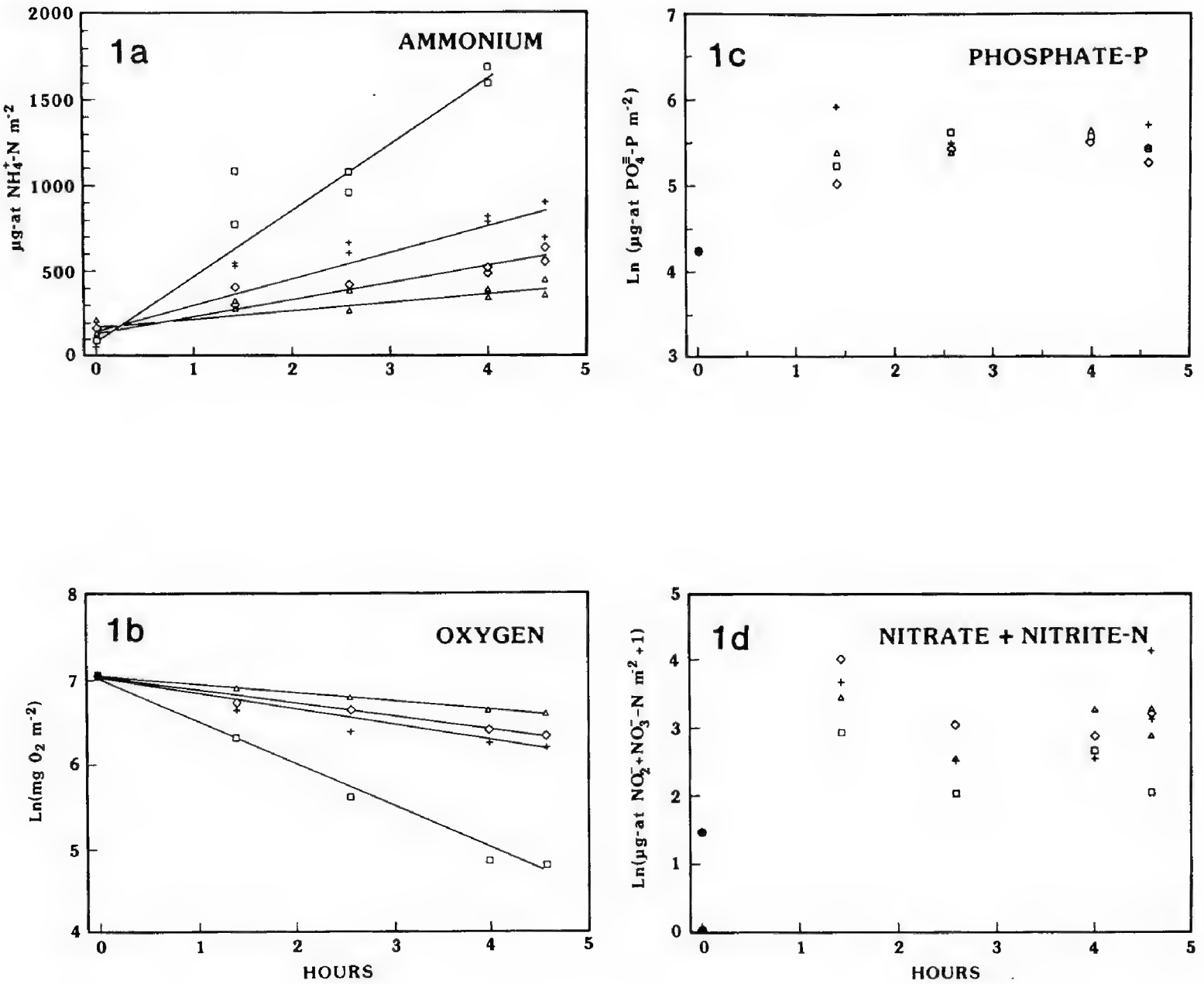

FIG. 1. Time courses of masses of ammonium (a), dissolved oxygen (b), phosphate–P (c), and nitrate+nitrite–N (d) in domes containing various densities of shrimp. Fitted regression lines are shown where significant relationships exist ($P < 0.05$). (Key to shrimp densities per m^2 bottom: square = 54, cross = 28, diamond = 14, triangle = 0). Regression statistics appear in Table 1.

System metabolism and nutrient flux in the absence of shrimp were normal for this site. Conditions in the control dome throughout the experiment and in all four domes prior to adding shrimp were not significantly different from measurements made the previous day during identical experiments conducted at the same site but without shrimp ($P > 0.05$; t-test for difference between two means assuming equal variances, Sokal and Rolhf 1969). Oxygen consumption in the control dome was 94.5 mg O_2 $m^{-2} \cdot hr^{-1}$, compared to 84.5 mg O_2 $m^{-2} \cdot hr^{-1}$ (S.E. = 2.1; $n = 3$) the previous day. Mean concentration of ammonia in the absence of shrimp was 1.83 µg-at NH_4–N L^{-1} (S.D. 0.69; $n = 33$) compared to 1.95 µg-at NH_4–N L^{-1} (S.D. = 0.89; $n = 15$) the previous day. Mean concentration of nitrate+ni-

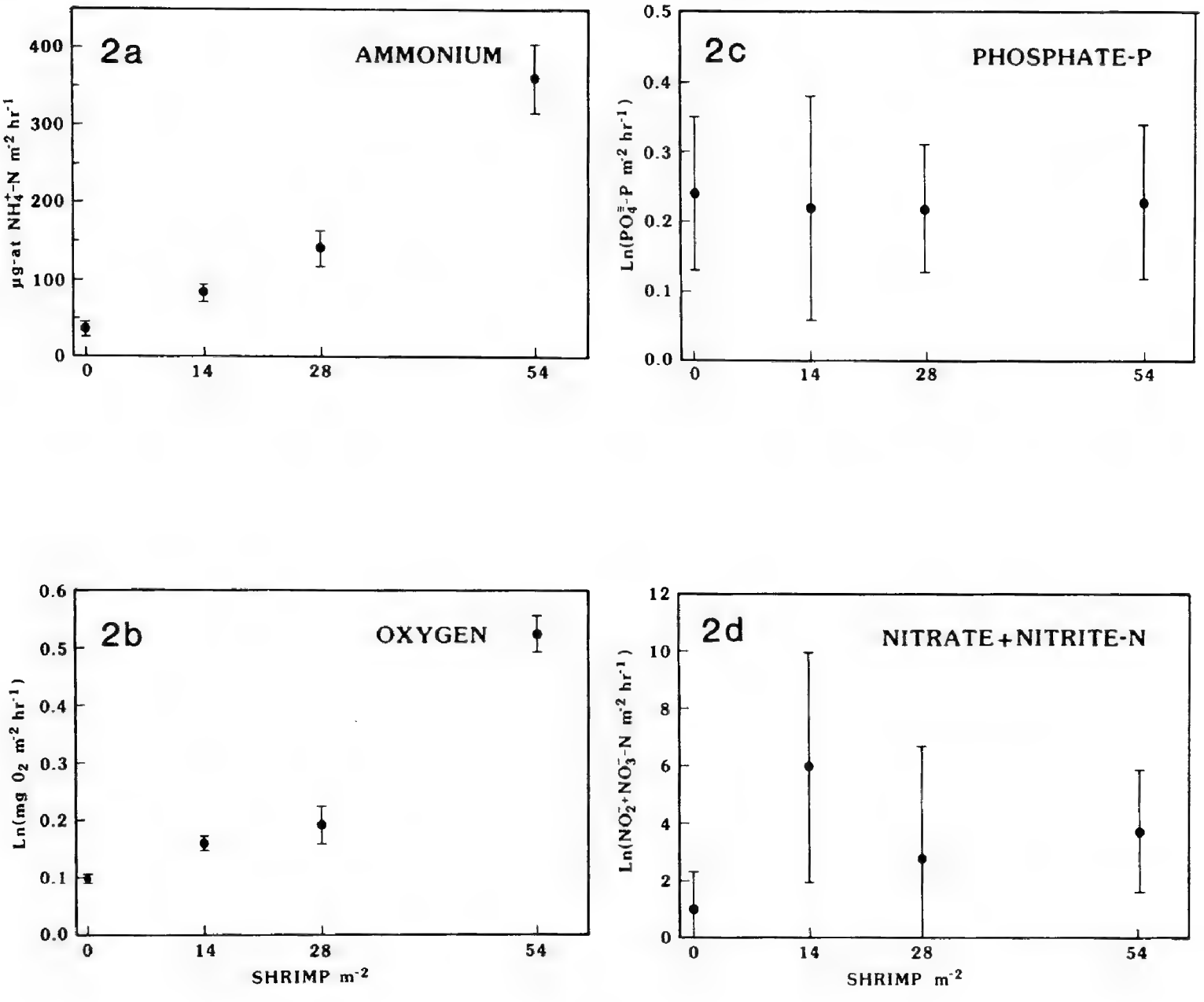

FIG. 2. Relationships between shrimp density in domes and flux of oxygen and nutrients across the sediment-water interface. Vertical bars denote ± one standard error.

trite–N from all 4 domes during the shrimp experiment was 0.18 µg-at NO_2+NO_3–N L^{-1} (S.D. = 0.11; n = 28) compared to 0.23 µg-at NO_2+NO_3–N L^{-1} (S.D. = 0.07; n = 18) the previous day. Phosphate–P was not measured the previous day, but mean concentration during the shrimp experiment was similar to values measured at the same site on other occasions (Hopkinson and Wetzel 1982).

Conditions in the domes did not have any visible effect on recaptured shrimp. Shrimp were seen to escape when divers lifted each dome at the end of the experiments, and even at highest densities divers failed to recapture more than one-third of them. By the end of the experiment, oxygen concentration in the dome containing 54 shrimp • m^{-2} (0.74 mg O_2 • L^{-1}) was below the level at which brown shrimp (*P. aztecus*; a closely related species) begin to show decreases in metabolism with decreasing oxygen concentration (3.0 mg O_2 • L^{-1}; Wang 1981). However, behavior and appearance of

shrimp recaptured from this dome did not differ detectably from shrimp from other domes. No mortality occurred in any of the domes. Divers searched the sediment beneath each dome after the experiment but found neither shrimp nor apparent burrows. White shrimp do not burrow as frequently or deeply as brown or pink shrimp (Williams 1958). Adult white shrimp kept in laboratory tanks with 8 to 10 cm sediment burrowed only rarely and never deeper than 3 to 5 centimeters (Vetter, unpublished data). The vertical flanges surrounding each dome and extending 10 cm into the sediment should have been sufficient to contain the shrimp and prevent escape during the measurements.

DISCUSSION

We have shown that strong pulses in system metabolism and ammonium flux can occur in the vicinity of penaeid shrimp aggregations. Two questions arise—1) are these pulses significant compared to rates and nutrient requirements estimated for components of the open system in the absence of shrimp, and 2) how strong are pulses likely to be in the open system (*i.e.*, what are the actual densities of shrimp in the nearshore zone), assuming dome rates reflect actual shrimp effects on benthic processes?

The first question can be answered by comparing rates in domes to existing estimates of heterotrophy and nitrogen flux in the nearshore zone. Only oxygen metabolism and ammonia flux are relevant, since shrimp had no apparent effect on nitrate or phosphate.

The second question cannot be answered with existing data, because the actual distribution and density of shrimp aggregations in this system are unknown. Our maximum density provides an upper bound; having bracketed the likely distribution of shrimp densities in the natural system, a rough estimate of "shrimp effects" could be derived for any density by regressing rate against shrimp density in each dome. Rulifson's (1981) results showed that penaeid shrimp in laboratory tanks (2.4 m diameter) tend to aggregate in groups of 4 to 20 shrimp $\cdot$ m^{-2}, corresponding roughly to our lower density (14 shrimp $\cdot$ m^{-2}). Even at half this density, ammonium regeneration could be 50% higher than measured in the absence of shrimp (Fig. 2a). Densities of migrating or feeding shrimp could be higher, if animals aggregate to exploit patchy food resources or to minimize risk of predation. Trawl records imply that white shrimp tend to be densely and patchily distributed in natural systems (Linder and Cook 1970). One of two boats fishing the same place at the same time often catches nothing, while the other fills its nets (Hildebrand 1954).

Commercially-exploitable (dense) aggregations of white shrimp persist for several weeks during late summer and early fall in the nearshore Georgia Bight (Harris 1974). It is during this season that system heterotrophy and apparent nutrient limitation are greatest (Hopkinson and Wetzel 1982).

Benthic metabolism measured in this system in the absence of shrimp is high, and comparable to previously reported rates from highly-productive estuarine and coastal marine systems (Pamatmat 1971, Smith 1973, Nixon *et al.* 1976, Boynton *et al.* 1980). This high rate increased by 50–100% even with low densities of shrimp (Table 1, Fig. 2b). Hopkinson and Wetzel (1982) demonstrated that the nearshore zone of the Georgia Bight is heterotrophic during summer and that the benthos (excluding motile macrofauna) accounts for about 25% of community metabolism. Incorporating shrimp as components of the benthic system substantially augmented the heterotrophic nature of localized regions in the nearshore zone. Consequently, allochtonous inputs from adjacent rivers and/or estuaries take on added importance as potential sources of organic matter to balance these heterotrophic requirements during late summer when shrimp are present in the system.

In addition to augmenting benthic respiration, the presence of adult white shrimp substantially increased ammonium regeneration. This accelerated transfer of inorganic nitrogen from localized areas of benthos to the nearshore water column could be important for two reasons—1) water column N:P ratios of 0.2:1 in the nearshore Georgia Bight during late summer when adult white shrimp are most abundant indicate that nitrogen supplies are limiting primary production in the system at this time (Hopkinson and Wetzel 1982), and 2) ammonium is the form of inorganic nitrogen preferred by most phytoplankton (Dugdale and Goering 1967, MacIsaac and Dugdale 1969, 1972, Eppley *et al.* 1973). If the high affinities for ammonium reported for oceanic phytoplankton (McCarthy and Goldman 1979) are also characteristic of phytoplankton populations in this nearshore system, these populations may benefit from a preferred, readily-available and exploitable source of inorganic nitrogen in the vicinity of shrimp aggregations.

Several studies have demonstrated that natural populations of algal cells are able to exploit such transient patches of concentrated nutrients (*e.g.*, Glibert and Goldman 1981, Goldman and Dennett 1985, Elrifi and Turpin 1985). Provided algal cells are in close proximity to the nutrient source and uptake rates exceed diffusion or mixing rates, the algae could benefit from this enhanced supply of inorganic nitrogen. The system we studied is a shallow coastal system well mixed by winds and tides. Phytoplankton could be regularly exposed to the sediment-water interface and uptake rates of nutrient-limited phytoplankton can be quite high (*e.g.*, Lehman and Scavia 1982).

Comparisons of ammonia flux from benthos with and without shrimp indicate that contribution by benthic systems incorporating shrimp can be significant. In the absence of shrimp, the benthos in the nearshore Georgia Bight supplies only 16% of phytoplankton populations daily requirement for inorganic nitrogen (Hopkinson and Wetzel 1982). Regeneration of nitrogen from benthos including shrimp was up to nine times greater than from systems without shrimp (359 versus 40 μg-at NH_4–N $\cdot$ m^{-2} $\cdot$ hr^{-1}). This increase could satisfy up to 98% of nearby algal cells' daily requirement for

inorganic nitrogen. While it is unlikely that densities as high as 54 shrimp • m^{-2} occur frequently in nature, substantial increases in ammonium flux were observed in all domes containing shrimp (Table 1). Even at the lowest density, which corresponds to densities observed in laboratory studies (Rulifson 1981), ammonia flux more than doubled (Table 1, Fig. 2b).

Our data suggest that a systems-level feedback loop can exist between penaeid shrimp, inorganic nutrient availability, primary production, and secondary production. Including shrimp as benthic components both increases total benthic metabolism, and results in greater remineralization of nutrients from the benthos. This in turn can stimulate primary productivity and hence secondary productivity in this nutrient-limited nearshore system.

Enclosure studies of this kind are obviously limited and unnatural in many respects; but the multiplicity of possible interactions between components in any natural ecosystem imply that simple extrapolations from laboratory studies may miss important factors. We tested this possibility by comparing metabolic rates and ammonium production by white shrimp under laboratory conditions (in isolation from the benthic system) with "per shrimp" effects estimated from our dome study.

All shrimp in our study were nearly identical in size (12.4 cm TL; S.D. = 1.5; $n = 27$), and rates in the control dome were similar to rates measured previously in the absence of shrimp. Consequently, rates of oxygen consumption and ammonia regeneration "per shrimp" can be calculated by regressing rate (flux • m^{-2} • hr^{-1}; untransformed data) against shrimp density (shrimp • m^{-2}). These "per shrimp" rates can then be compared to rates measured under laboratory conditions.

Differences were evident. "Per shrimp" effects in the intact system were 3.8 mg O_2 • $shrimp^{-1}$ • hr^1 (S.E. = 0.4, $n = 4$) and 6.0 μg-at NH_4–N • $shrimp^{-1}$ • hr^{-1} (S.E. = 0.5; $n = 4$). Both rates were lower than average rates determined in the laboratory with shrimp of the same size, 6 to 8 hours after capture from an adjacent estuary (5.8 mg O_2 • $shrimp^{-1}$ • hr^{-1}; 15.4 μg-at NH_4–N • $shrimp^{-1}$ • hr^{-1}, Vetter 1983). Temperature in the laboratory studies ranged from 24 to 27C and salinity from 25 to 31‰; compared to 25C and 32‰ in the field experiment. Simply adding lab rates to control rates would have over-estimated the observed flux, in both cases.

Several factors could have contributed to the discrepancy in oxygen metabolism and ammonia regeneration. Ammonia flux may not have been corrected for properly in dark bottle water-column blanks, because such blanks may not fully simulate nutrient dynamics in domes with rates elevated substantially over ambient levels. Also, total flux of ammonium could have been masked by rapid chemical or biological re-utilization of regenerated ammonia, thereby reducing apparent net flux. Oxygen consumption rates would not be masked by oxygen production within the darkened domes, but it is possible that both metabolism and ammonium flux were affected by differences in feeding histories of shrimp in domes compared to shrimp in laboratory experiments. Shrimp in the field experiment had not been fed since their capture about 18 hours before release into

the domes. Shrimp in the laboratory experiments had full guts when captured, and rates reported above are for resting animals after 6 to 8 hours in laboratory metabolism chambers. Oxygen consumption had decreased 44% (from 6.8 mg $O_2 \cdot \text{shrimp}^{-1} \cdot \text{hr}^{-1}$) and ammonia excretion had decreased 66% (from 35 μg-at $NH_4-N \cdot \text{shrimp}^{-1} \cdot \text{hr}^{-1}$) during this time (Vetter 1983). It is possible that after 12 additional hours, rates in the metabolism chambers might have approached rates inferred from the dome experiment.

But this assumes only direct contributions by shrimp to oxygen and ammonium flux. Changes in benthic system metabolism and nutrient flux in the presence of shrimp are not necessarily due only to direct effects. Indirect effects due to responses by other system components to the presence of shrimp can also occur. Had shrimp released into the domes been recently fed, direct contributions to oxygen and ammonia flux might have been greater, but indirect effects of sediment disturbance and feeding by hungry penaeid shrimp might have been less. Direct effects cannot be separated from indirect effects in the present study because we specifically designed the experiment to study responses of an intact system. We wanted to measure integrated effects of hungry adult white shrimp migrating through an area, aggregated in various densities, under natural or near-natural conditions. Determining direct contributions by each shrimp was not our objective; rather we wished to investigate overall differences that might arise in our estimates of nutrient flux, when including these macrofauna as an additional component of the benthos.

In the nearshore zone of the Georgia Bight, the presence of adult white shrimp increased the heterotrophic nature of the system and enhanced ammonium flux in localized patches. If present on time and space scales useful to algae, the additional ammonia could satisfy nearly all the nitrogen requirements of nearby phytoplankton during late summer in this nitrogen-limited system. Our study does not explain the mechanisms by which effects are generated in the intact system. But it does demonstrate that system metabolism and nutrient flux can be significantly affected by integrated effects of motile macrofauna in naturally-occurring densities.

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RELATIONSHIPS BETWEEN POSSIBLE AVAILABLE FOOD AND THE COMPOSITION, CONDITION AND REPRODUCTIVE STATE OF OYSTERS FROM GALVESTON BAY, TEXAS[1]

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ABSTRACT

Possible food for oysters was measured as a food index. The food index was defined as the percentage food (food = lipid + carbohydrate + protein) in the total seston. Highest condition index values (C.I. = dry weight/mantle volume × 100) of oysters were not related to the time of greatest available food. The food index was, however, correlated with the gonadal index (G.I. = gonadal thickness/adductor muscle diameter) of oysters. The greatest amount of available food was present during the time of presumed greatest energy demand, namely the period of gametogenesis.

The concept of the storage cycle is applicable to *Crassostrea virginica*. Changes in the oysters' composition and in condition and gonadal indices support the hypothesis that stored glycogen is converted into the lipid reserves of the developing eggs.

The percent carbohydrate and percent lipid content of oysters are positively correlated with the condition index. Increasing carbohydrate levels and condition indices are indicative of oysters in the fattening stage. The increase in lipid levels began in the early spring as carbohydrate levels began to decline. High lipid levels and high gonadal indices occur as a prelude to spawning. High percent protein values and low condition and gonadal indices are characteristics of oysters that have spawned.

Changes in the condition and gonadal indices of oysters are temperature-related. Initial spawning apparently occurred at a temperature between 21° and 25°C.

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INTRODUCTION

A number of studies have been conducted on seasonal changes in the proximate composition of *Crassostrea virginica*. Compositional studies on

the American oyster by Lee and Pepper (1956) and Lee, Kurtzman and Pepper (1960) showed that dry solids, percent fats, and percent carbohydrates were lowest in the summer and fall and highest in the spring just prior to spawning. An inverse relationship between percent protein and percent carbohydrate was established; that is, percent protein decreased to a minimum in spring (May) when other constituents were at the seasonal maximum, then increased to highest values in the summer (August). Similar results were obtained by Sidwell, Loomis and Grodner (1979). Nutritional materials derived from food may be stored and later used for reproduction. Thus, although the nutritional state of a bivalve relates to the nutritional milieu of the organism as well as to its reproductive status, few studies have been conducted on the relationships between seasonal changes in bivalve condition, reproductive state and available food.

Bayne (1976) has summarized the results of numerous biochemical studies on bivalves. The general pattern is that nutrient reserves are accumulated when food is abundant. These reserves may later be used to meet energy needs when food is scarce or to support the energy demands of gametogenesis. The conversion of a bivalve's food to glucose, glucose to stored glycogen, and the eventual production (from the glycogen store) of lipids used for reproduction is called the "storage cycle" (Giese 1959, Gabbot 1975).

The data of Hopkins, Mackin and Menzel (1954) indicate that the condition index (Hopkins 1949) of Louisiana oysters was greatest in early spring (March) and corresponded to the highest percentage of glycogen by wet weight. The condition index varies directly with the glycogen content, since the weight of the oyster meat and glycogen content are greatest prior to spawning, and both are lowest after spawning. It is reasonable to expect that variations in the proximate composition of the oyster are related to changes in condition and gonadal indices and water temperature.

The objectives of the present work were:

(i) To carry out a field sampling study over an annual cycle to provide a more thorough understanding of the relationship of oyster condition and its natural food supply.

(ii) To determine seasonal changes in the proximate composition of the oyster.

(iii) To establish a relationship between the proximate composition of oysters and condition and gonadal indices.

(iv) To clarify some of the relationships between water temperature and oyster composition and reproductive state.

METHODS

WATER TEMPERATURE

Water temperature was measured monthly to the nearest 0.1°C using a mercury thermometer. The period of the study was September 1980 to September 1981.

ANALYSIS OF AVAILABLE FOOD

Available food for the oyster was measured twice a month (semi-monthly) as a food index. The food index was defined as the percentage food (food = lipid + carbohydrate + protein) in the total seston (Widdows, Fieth and Worrall 1979). The extraction and analysis of lipid, carbohydrate and protein is a modification of methods of Holland and Gabbot (1971) and is similar to the methods described herein for the analysis of the oyster tissue. Details of the extraction and analysis of the food index (and more details of the synoptical seston data) are provided by Soniat (1982) and Soniat, Ray and Jeffrey (1984). Weighted average food index (W.A.) values for each month (except the first and last) are calculated as follows:

$$\text{W.A.} = \frac{a + 2b + c}{4}$$

where a is the average food index value for the previous semi-monthly sample period, b is the average food index value for the month (*i.e.* the average value measured on the same day that the oysters were collected), and c is the average food index value for the following semi-monthly sample period. The weighted average food index for the first month ($2b+c/3$) and last month ($a+2b/3$) were similarly calculated.

ANALYSIS OF OYSTERS

Oysters were collected by tonging monthly from April Fool Reef, located in the west-central sector of Galveston Bay (see Soniat 1982 for details). The oysters were culled and cleaned of attached epifauna and adhering sediment. The length (distance from the umbo to the bill) of the right valve was measured to the nearest millimeter. The total volume of two sets of ten oysters each was determined by displacement. After the oysters were opened and the meats removed, the volume of the shells was likewise measured. The difference between the volume of the whole oysters and the volume of the shells represents the volume of the mantle cavity (Galtsoff 1964).

Gonadal thickness (Galtsoff 1964) and adductor muscle diameter were measured and used to calculate a gonadal index (G.I.) according to the following formula:

$$\text{G.I.} = \frac{\text{average gonadal thickness (mm)}}{\text{average diameter of adductor muscle (mm)}} \times 100$$

Wet and dry weights of the sets of oysers were determined (dry weight was determined after the oysters were frozen at $-20°C$ and freeze-dried). A condition index (C.I.) was calculated according to the equation of Hopkins (1949):

$$\text{C.I.} = \frac{\text{dry weight (gm)}}{\text{mantle volume (cc)}} \times 100$$

Three aliquots of approximately 0.5 g from each set of oysters were used to determine weight of the inorganic matter (Lee and Pepper 1956). A second subsample of about 1.0 g was used for the determination of lipid, carbohydrate and protein levels. The extraction and analytic procedure was a modification of that of Holland and Gabbot (1971). The subsample was homogenized in 100 ml of a 2:1 chloroform:methanol mixture and filtered using a Gelman A/E glass fiber filter. The filtrate was evaporated at 40–50°C overnight and subsequently weighed. The residue was treated with 5% cold trichloroacetic acid, shaken for 5 min. and allowed to stand for 10 min. at 4°C. After filtration (Gelman A/E glass fiber filter) the filtrate was analyzed for carbohydrate using the method of Strickland and Parsons (1972) with anhydrous dextrose as a standard. One hundred ml of 1N NaOH was added to the remaining residue. The sample was heated at 56°C for 30 minutes . The protein concentration was then determined by the method of Lowery, Rosenbrough, Farr and Randall (1951) using bovine serum albumen as a standard.

Three measurements were made on the single extraction from each set of ten oysters (see Soniat 1982 and Soniat *et al.* 1984).

RESULTS

WATER TEMPERATURE

Temperature varied from 9.3°C in February, 1981 to 30.1°C in August, 1981. Temperature values are given in Table 1.

TABLE 1

Monthly water temperature and weighted average food index (WA) values.

Month	WA	Temperature (°C)
Sept. 1980	1.4	28.9
Oct.	1.2	25.0
Nov.	1.0	19.5
Dec.	1.9	15.1
Jan. 1981	1.6	14.1
Feb.	3.9	9.3
Mar.	4.6	18.9
Apr.	3.3	21.3
May	4.7	25.1
June	3.9	27.7
July	7.0	30.0
Aug.	4.0	30.1
Sept.	3.5	28.0

AVAILABLE FOOD

Weighted average food index values ranged from 1.0% for November, 1980 to 7.0% for July, 1981 (Table 1). The semi-monthly data are plotted and are discussed under the inter-relationships section. Although the food index varied markedly from sampling day to sampling day, values were generally higher in the spring and summer than in the fall and winter.

OYSTERS

The length of the oysters used in the study ranged from 7.0 to 13.6 cm. Protein always comprised the majority of the percent dry weight of oyster tissue (Fig. 1). The average percent protein was 45.8. Protein values ranged from a low in May of 34.8% to a high in September 1981 of 62.1%. Late

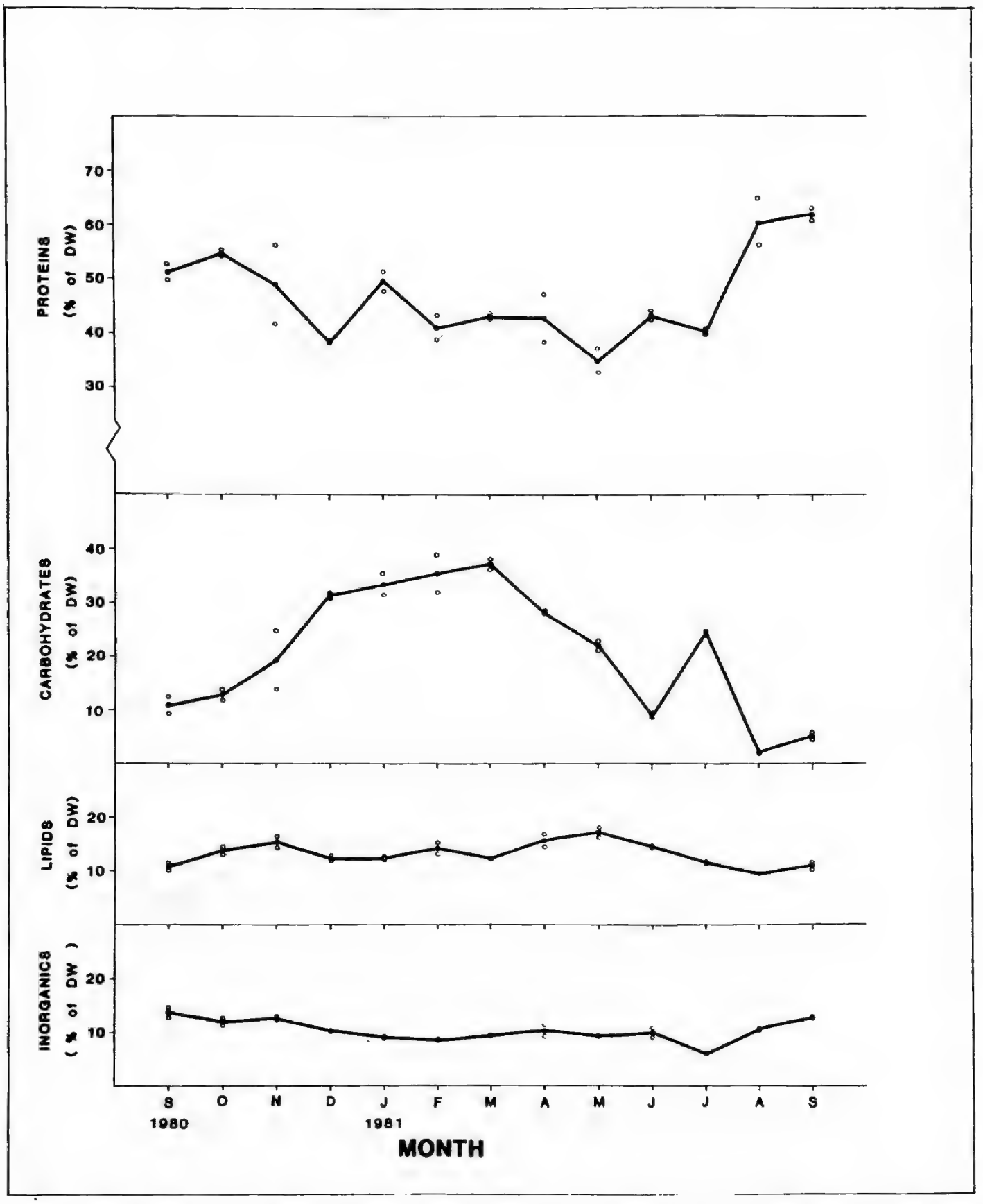

FIG. 1. Monthly levels of protein, carbohydrate, lipid and inorganic matter expressed as a percent of oyster dry weight (DW). Mean monthly values are plotted as the closed circles. The two data points used to calculate the mean are plotted as the open circles.

summer and early fall values were significantly higher than those at other times of the year. Percent carbohydrate averaged 20.8% over the sampling period. Carbohydrate values varied more than any of the other major body-constituents (Fig. 1). Carbohydrate levels ranged from a March high of 37.0% to an August low of 2.2% (Fig. 1). Lipid values averaged 13.0% and

ranged from 17.0% (May) to 9.4% (August). Percent inorganic values (Fig. 1) were highest in late summer. The average value for inorganics was 10.2%; values ranged from 5.9% (July) to 13.7% (Sept., 1980.)

Average values of wet weight and dry weight were 112.0 gm and 21.6 gm, respectively. Percent water ranged from 75.3% in March to 85.1% in September 1981 and averaged 81.7%.

The condition index averaged 6.5 over the study period. Condition index ranged from a September 1981 low of 3.3 to a March high of 9.9 (Fig. 2). Condition index from January to April was significantly higher than at other times of the year.

The gonadal index had an average value of 6.8. Values ranged from a July high of 11.3 to a January low of 1.3 (Fig. 2). Highest gonadal indices were measured during spring and summer.

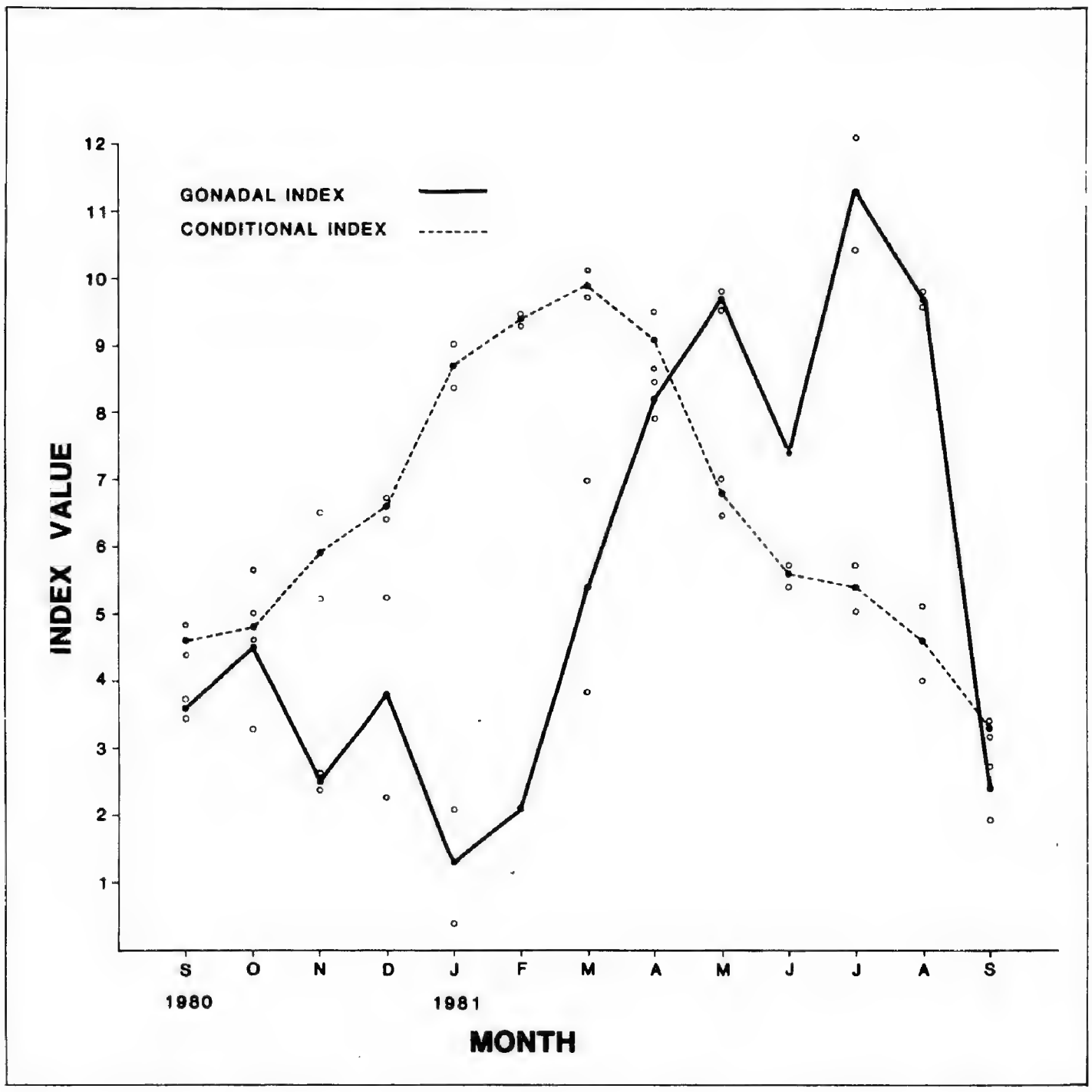

FIG. 2. Monthly means for gonadal and condition indices. Mean monthly values are plotted as the closed circles. The two data points used to calculate the mean are plotted as the open circles.

Kruskal-Wallis tests were (Hull and Nie 1981) significant for all the oyster measurements ($p < 0.05$). Individual month-to-month differences are easily gleaned from Table 2. The results of multiple comparisons (Dunn 1964)

TABLE 2

Mean rank values from the Kruskal-Wallis analysis for the oyster data. Mean rank values >12.9 between two sample days are significant ($\alpha = 0.15$).

Month	Carbohydrate	Protein	Lipid	Inorganics	Gonadal Index	Condition Index
Sept. 1980	8.00	18.00	4.50	25.50	11.50	5.00
Oct.	9.00	20.50	16.00	20.00	12.50	6.00
Nov.	13.00	15.50	21.50	21.50	7.50	13.00
Dec.	20.00	3.50	11.50	14.50	10.00	15.50
Jan. 1981	21.50	17.00	11.00	7.00	2.25	20.00
Feb.	24.00	9.00	19.00	3.50	4.25	22.50
Mar.	24.50	12.00	12.00	11.50	14.50	25.50
Apr.	17.50	10.00	22.00	13.00	19.50	22.00
May	12.50	1.50	25.00	8.50	22.00	16.50
June	5.50	12.00	19.50	11.50	17.50	11.75
July	15.00	7.50	7.00	1.50	25.50	10.25
Aug.	1.50	24.50	1.50	14.50	23.00	6.00
Sept.	3.50	24.50	5.00	23.00	5.50	1.50

between highest mean ranks versus lowest mean ranks were all significant at the $p < 0.005$ level or less. Overall trends are easily visualized in Fig. 3.

INTER-RELATIONSHIPS

Table 3 gives values for the Spearman correlation coefficients between water temperature, the food index and the various oyster parameters. The condition index and the percent carbohydrate of oysters were negatively correlated with temperature, whereas the gonadal index was positively correlated with temperature. Oyster condition index values were thus positively related to carbohydrate levels. Lipid values also showed a positive correlation with the condition index. Inorganic composition varied directly with percent protein and indirectly with percent carbohydrate and the condition index. Protein values varied inversely with lipid and carbohydrate levels as well as with the condition index. The food index was directly correlated with the gonadal index and inversely correlated with the concentration of inorganics.

DISCUSSION

The values obtained for the proximate composition of the Galveston Bay oysters are quite similar to values reported for other Gulf coast oysters

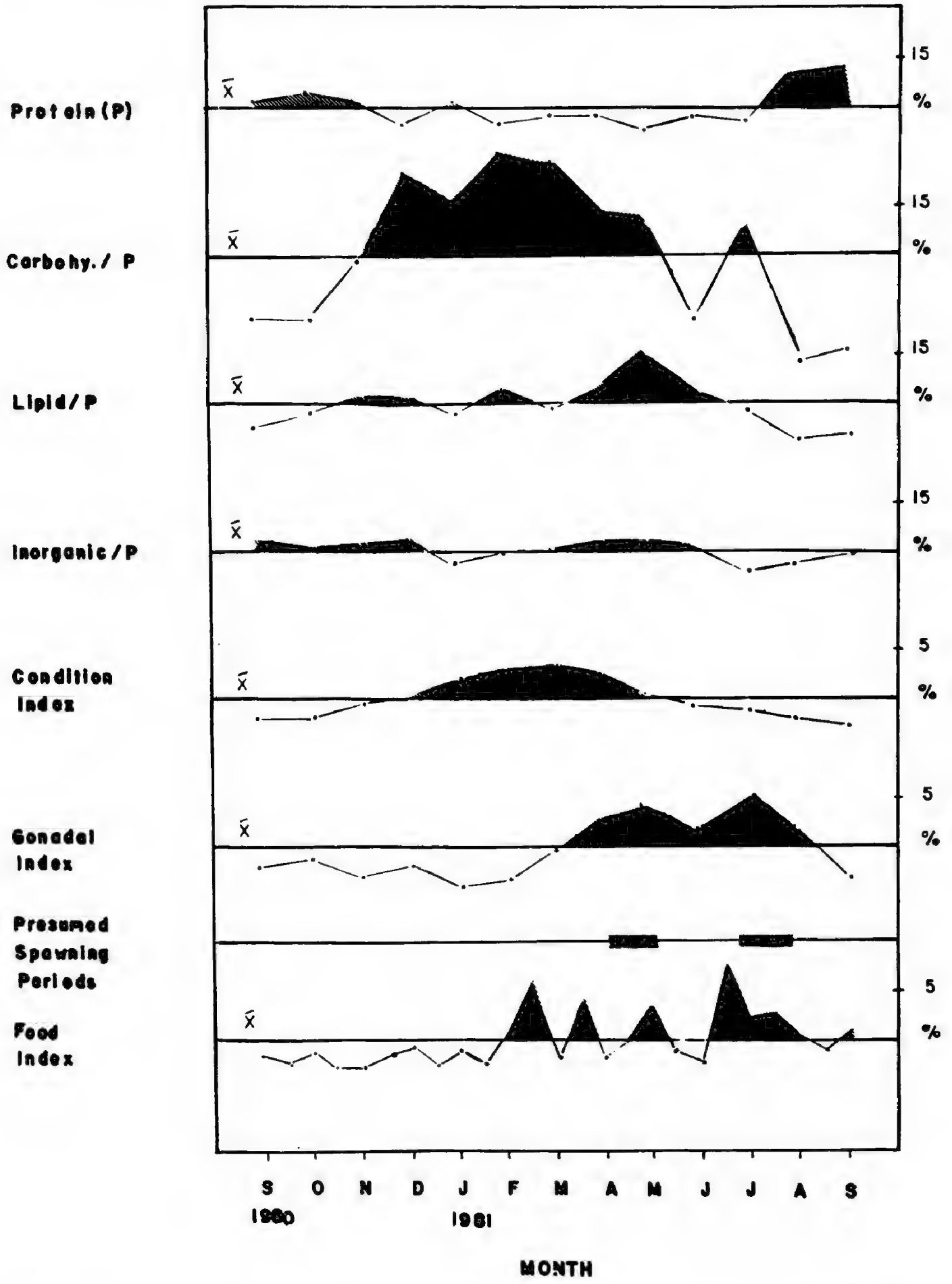

FIG. 3. Seasonal cycle in oyster composition, condition, and reproduction as well as the environmental food index. Oyster parameters are given as monthly values, and the food index is shown in terms of semi-monthly values. For each parameter the grand mean value is shown as the solid horizontal line, and the monthly or semi-monthly deviations from the mean are plotted as the percent deviation from the annual mean. To facilitate comparison of the different parameters, the areas under the positive deviations have been shaded.

TABLE 3

Spearman rank correlation coefficients between the various oyster measurements and the weighted average food index (WA) and water temperature (T). C = carbohydrate, P = protein, L = lipid, I = inorganics, GI = gonadal index, CI = condition index. N = 13.

	C	P	L	I	GI	CI	WA	T
C	-	-0.63*	0.33	-0.64**	-0.22	0.89***	0.14	-0.80***
P	-	-	-0.51	0.66**	-0.33	-0.64**	-0.45	0.36
L	-	-	-	-0.30	0.08	0.61*	-0.03	-0.46
I	-	-	-	-	-0.22	-0.64**	-0.64**	0.33
GI	-	-	-	-	-	-0.10	0.61*	0.60*
CI	-	-	-	-	-	-	0.20	-0.79***
WA	-	-	-	-	-	-	-	0.28

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

(Hopkins *et al.* 1954, Lee and Pepper 1956, Sidwell *et al.* 1979). Protein tends to remain fairly constant whereas carbohydrate and lipid vary seasonally (Lee and Pepper 1956).

Carbohydrate shows the most dramatic change with a major peak occurring during the winter and spring (December–May) and a minor peak in July. The larger peak represents an accumulation of glycogen preceding the first spawning, and the secondary peak may represent reserves prior to a second late summer spawning period. Multiple peaks have been observed by Hopkins *et al.* (1954) and by Lee and Pepper (1956), but neither of these authors discussed the significance of the minor peaks. Identification of the second peak with repeated spawning is consistent with the results of Pieters, Klytmans, Zandee and Cadée (1980). These workers found that in the blue mussel, *Mytilus edulis*, the biochemical composition is closely associated with short-term changes in its gametogenic cycle.

Seasonal changes in lipid levels are consistent with the results of Lee and Pepper (1956) and Sidwell *et al.* (1979). Lipid levels increase in spring, and especially late spring, when the glycogen reserves are decreasing and the gonadal index is becoming elevated. This suggests a conversion of stored glycogen to lipid to be stored as a high energy source in the eggs. Unfortunately, sex differences in lipid levels are not available.

Inorganic levels obtained in the present study are also consistent with values reported in the literature (Lee and Pepper 1956, Sidwell *et al.* 1979). Although inorganic matter in the gut could influence the results, this contamination is not likely very great since the inorganic content tends to vary with protein content, as expected. Lee and Pepper (1956) and Sidwell *et al.* (1979) suggested that high levels of inorganics may be related to salinity. However, the association between oyster inorganics and water salinity in this study is not a close one. As Sidwell *et al.* (1979) suggest, there may be a greater accumulation of sandy material in the gut during certain times of the year. In the present study turbid conditions were especially prevalent

during the fall when the inorganic content of the oyster was generally elevated (Fig. 1).

Changes in the proximate composition of oysters are associated with changes in the annual cycles of fattening, storage and reproduction. The fattening phase is characterized by high condition indices, increased percent tissue dry weights and elevated levels of carbohydrate (Fig. 3). This phase occurred during the cooler months of the year as a prelude to spawning.

The condition index was also correlated with lipid levels of oysters (Table 3). The gonadal index of the oysters began to increase in early spring (Fig. 3). The transition from stored glycogen to lipid reserves in the developing eggs of *M. edulis* is called the "storage cycle" (Giese 1959, Gabbot 1975). The results of the present study are consistent with the hypothesis of a carbohydrate-lipid storage cycle in marine bivalve molluscs. Such a storage cycle seems to exist in *C. virginica*.

With the onset of spawning, the percent lipid and the gonadal index of the oyster decline as sexual products are released to the environment. Spent oysters show low lipid and carbohydrate levels. The percent protein is consequently elevated (Fig. 3). Low condition and gonadal indices (Fig. 3) and an increased percent water content are indicative of the spent oysters.

In an idealized sequence of events, the reproductive cycle of bivalves includes vegetative, growth and gametogenesis, maturation, spawning and resting stages (Sastry 1975). Resting and vegetative stages are associated with low gonadal indices. The stage of growth and gametogenesis is characterized by increasing index values. During maturation, the gonadal index is at its peak. Decreasing index values are found in spawning bivalves. A single spawning in oysters, however, is probably an exception rather than the rule (Chestnut 1948). The results of the present study show two peaks in the gonadal index of oysters. These peaks occurred in May and July, and probably represent two separate spawnings.

One factor which complicates the interpretation of the gonadal index data is the low salinity which occurred from mid-June to mid-July. Butler (1949) observed an inhibition of gametogenesis in oysters exposed to a salinity of less than 6‰. He suggested that the suppression of gonadal activity was attributable to a decrease in available food rather than to a direct inhibition of sexual activity by the less saline water. In the present study, the summer low in the gonadal index value preceded the freshet, food values remained high during the period of freshwater influence, and the gonadal index showed a definite increase. Thus, there was no evidence of reabsorption of gonadal material due to the low salinity water.

The interaction of temperature, gonadal maturation and spawning in oysters has received considerable attention (Hopkins 1931; Loosanoff 1942, 1969; Ingle 1951; Loosanoff and Davis 1950, 1951, 1952a, 1952b). In the present study, the gonadal index increased rapidly from February to April (Fig. 2) as the temperature rose from about 9° to 21°C. The first spawning at April Fool reef presumably occurred between early April (21°C) and early

May (25°C). Hopkins (1931) suggested that in Offatts Bayou (Galveston) spawning started when the water temperature reached 25°C. After what has been interpreted as the initial spawning period, the gonadal index decreased but did not reach winter levels (Fig. 2). This indicates that the oysters did not completely spawn out. High gonadal indices in July and August were followed by a very low value in September, 1981. By September, the oysters seemed completely spawned out.

Curiously, the period of highest food indices did not correspond to the time of most rapid glycogen accumulation and increasing condition indices. The food index was correlated, however, with the gonadal index. Strictly speaking, the food index is a measure of available food for bivalves only if one assumes (as did Widdows *et al.* 1979) that the animal has no ability to preferentially ingest organic material from the seston. Recent evidence suggests that a number of bivalves, including *C. virginica*, are able to ingest organic material in excess of its proportion in the seston (Kiørboe and Møhlenberg 1981; Newell and Jordan 1983). However, the food index is correlated with food (the sum of lipid + carbohydrate + protein concentrations in the seston) and both should correlate with oyster production (see Soniat *et al.* 1984).

The relationship between the food index and the gonadal index is not without precedent; a close relationship between available food and the production of ripe gametes was also observed by Lubet (1959). There is little doubt that the period of gametogenesis is a time of high energy requirement. This assertion is corroborated by the significant relationship which has been established between the rate of oxygen consumption and gametogenesis in bivalves (Bayne and Widdows 1978, Vahl 1978, Newell and Bayne 1980). However, from the present study, it cannot definitely be concluded that the energy associated with high food levels in the environment fuels the gametogenic process. As Gabbot (1976) claims, in all or nearly all of the examples cited in the literature, including data for *C. virginica*, the accumulation of glycogen precedes gonadal development. This stored glycogen is later used for gametogenesis. The decrease in the condition index (and the carbohydrate reserve) of oysters as the gonadal index increases supports this conclusion (Fig. 3). Gametogenesis and spawning, however, may require energy in excess of that stored. High levels of food may be especially important to subsequent spawning efforts. Seed (1976), for example, reports that mussels growing in favorable feeding conditions (*e.g.* the low shore) after initial spawning, frequently re-attain gonadal index values comparable to values attained in the spring. In mussels situated in poor conditions (*e.g.* the high littoral), full re-ripening is not as common. In the present study, full re-ripening apparently occurred. In fact, the July sample of oysters showed the highest gonadal index value. The timing of the sample, of course, influences this result. The May sample, for example, was probably taken after spawning had begun. The positive correlation between the food and gonadal indices, the high levels of food available in the spring

and summer, and evidence of the re-ripening of the gonads in summer support the contention that ambient food in the spring and summer was important in supporting gametogenesis and spawning.

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FIRST RECORD OF THE SPIONID POLYCHAETE *BOCCARDIELLA LIGERICA* (FERRONNIÈRE, 1898) FROM THE GULF OF MEXICO

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ABSTRACT

The spionid polychaete *Boccardiella ligerica* (Ferronnière, 1898), with a worldwide distribution in brackish waters, is recorded for the first time from the Gulf of Mexico. Included are a description of the species, comparison to a similar species, *B. hamata* (Webster, 1879), and ecological notes from collecting sites.

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INTRODUCTION

Boccardiella ligerica is a small, brackish-water spionid polychaete previously reported from western Europe, South Africa, California, West Indies, Uruguay and Argentina (Blake 1983). Because the original description of *Boccardia ligerica* Ferronnière, 1898 was ambiguous concerning the distribution of branchiae, the species was redescribed by Blake and Woodwick (1971) and synonymized with *Polydora redeki* Horst, 1920. Light (1977) referred specimens reported from San Francisco Bay as *Boccardia* near *uncata* (Hartman 1954) and *Polydora uncata* (Filice 1958) to *Boccardia ligerica*. Blake and Kudenov (1978) included *Polydora uncatiformis* Monro, 1938 as a synonym of *Boccardia ligerica* and transferred the species to the new genus *Boccardiella*, based on branchiae beginning anterior to setiger 5 and setiger 5 having only one kind of modified spine. *Boccardiella ligerica* was collected in the Aransas National Wildlife Refuge, Texas, but was identified as *Boccardia hamata* (Harper 1973, 1976). This is the first published record of *Boccardiella ligerica* from the Gulf of Mexico.

DESCRIPTION

BOCCARDIELLA LIGERICA (FERRONNIÈRE, 1898)

Figure 1

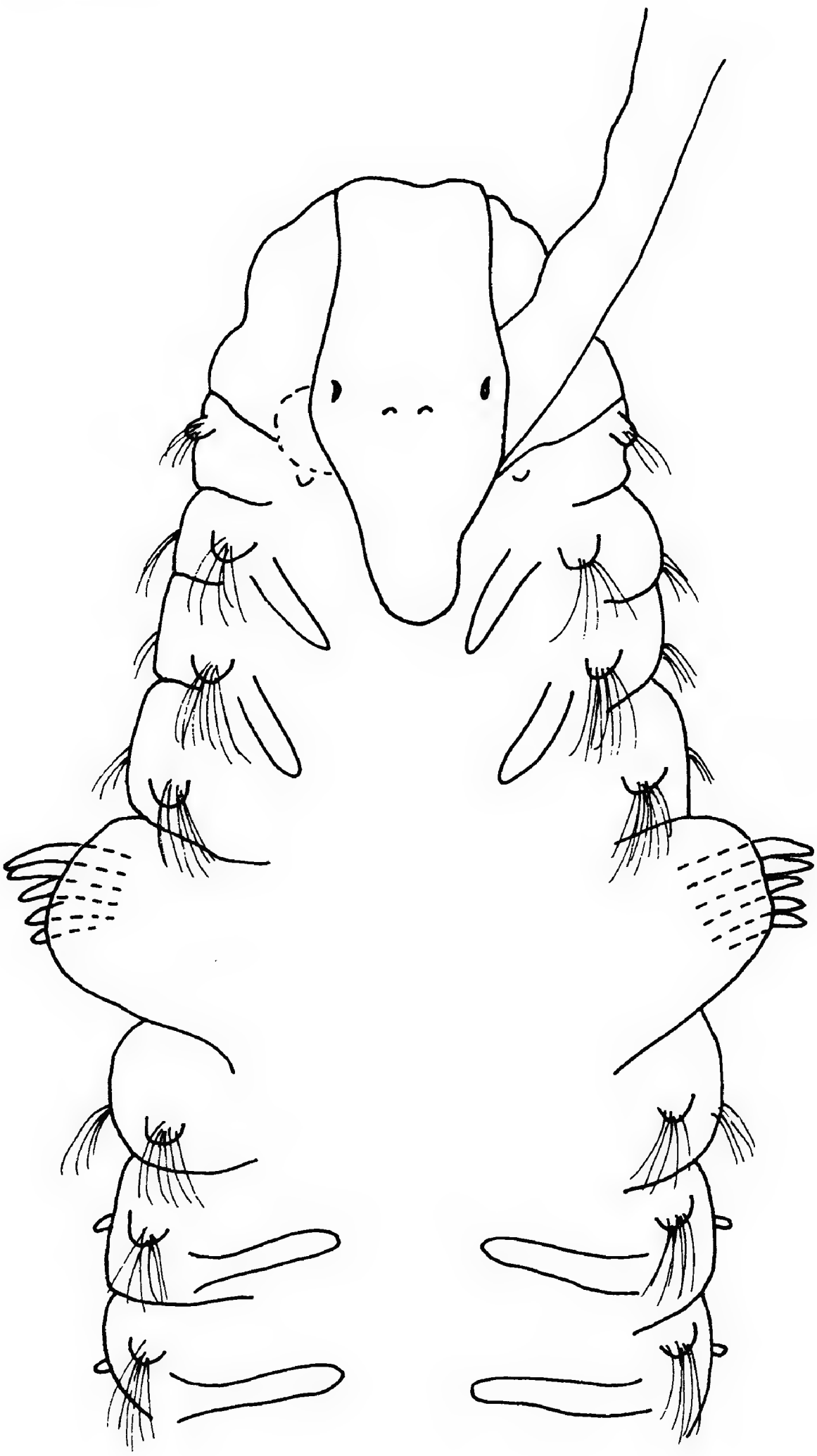

FIG. 1. *Boccardiella ligerica*. Dorsal view, anterior end.

B. ligerica has a reported length up to 16 mm, width of 0.75 mm, and about 70 segments (Light 1978). The largest specimen collected along the Texas coast (at the Aransas National Wildlife Refuge) was 62 segments. The prostomium bears two pairs of eyes arranged in a crescent (Fig. 1). Anteriorly, the prostomium is entire to slightly incised; posteriorly, it extends as a caruncle to setiger 2 or 3. There is no occipital antenna. A pair of tentacular palps are located posteriorly on the large cradling peristomium. Large cirriform branchiae are present on setigers 2 and 3 and from 7 to as far as 24 (range of my samples 14–24; mode 18). Anteriorly, parapodia have small, well-developed postsetal lamellae in both rami, except for setiger 1 where the notopodium is reduced to an achaetous lobe, and on setiger 5 where postsetal lamellae are lacking. Notopodial postsetal lamellae become indistinct in middle sections but reappear near the posterior end. Neuropodial postsetal lamellae are reduced to low ridges from setiger 7. The modified setiger 5 has large, blunt, simple spines that alternate with geniculate and limbate companion setae. Fascicles of capillary setae are located above and below the row. Notosetae are limbate capillaries on segments 2 through 4 and from 6 until the posterior end where the capillaries are joined by one medially-directed boathook spine. I found the segment on which the first spine appears to be variable. Neurosetae on segments 1–4 and 6 are limbate capillaries; from setiger 7 on, the capillaries diminish in number, becoming replaced by bidentate hooded hooks. The flat, unnotched pygidium bears a dorsal anus and a pair of posterolateral anal cirri.

DISCUSSION

SIMILAR SPECIES

B. ligerica closely resembles *B. hamata*, which has led to misidentifications in California (Light 1978) and Texas (Harper 1973, 1976). *B. hamata* differs from *B. ligerica* in having small branchiae on setiger 6 and branchiae not fully developed until setiger 9 (Light, 1978). The pygidium of *B. hamata* is divided into two lobes, each bearing a terminal process.

ECOLOGICAL NOTES

I collected 842 specimens of *B. ligerica* from the brackish-water marsh areas in Sea Rim State Park near Sabine Lake, Texas (Fig. 2). Benthic samples were collected monthly between September 1978 and August 1979, but the majority of specimens were obtained in September and November 1978 (613 and 213 individuals, respectively). During the two months, bottom salinities ranged from 10 ppt to 18 ppt, and bottom temperatures ranged from 25°C to 31°C. Almost all specimens came from a site at a pass with a hard, silty-clay bottom (other areas sampled were mostly soft-bottom). In Europe, this species has been reported from mudflats (Light 1978) and from

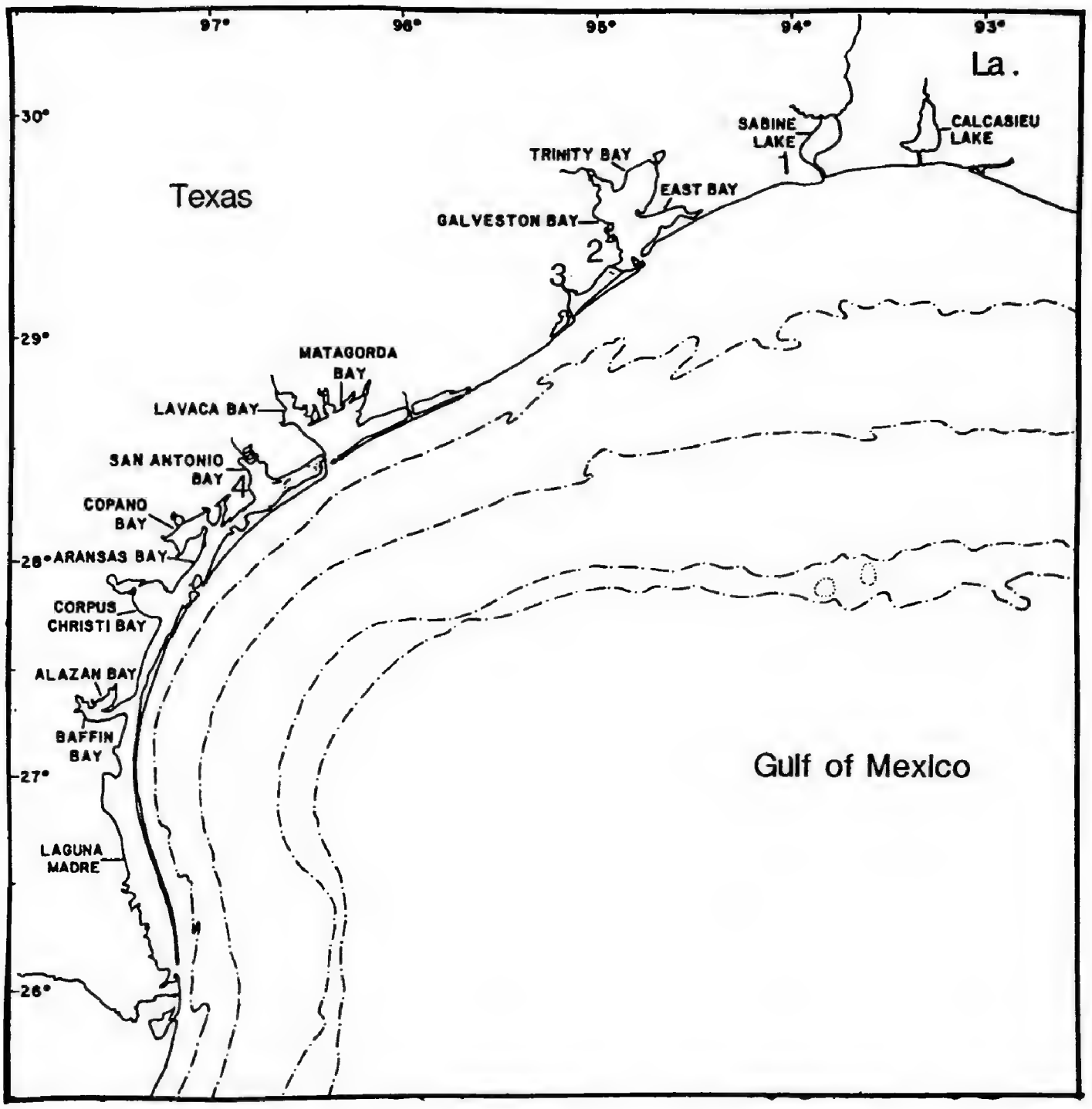

FIG. 2. Collection sites: (1) Sea Rim State Park, (2) West Bay, Galveston County, (3) New Bayou, Brazoria County, and (4) Aransas National Wildlife Refuge, San Antonio Bay system.

clay bottoms (Hempel 1957a, b [as *Polydora redeki* Horst]; Rullier 1960 and Eliason and Haahtela 1969; [as *Polydora (Boccardia) redeki* Horst]). In California, *B. ligerica* (reported as *Polydora uncata* Berkeley) exhibited no substrate preference among sand, mud and shell (Filice 1958).

Additional specimens were also available for study. *B. ligerica* (as *Boccardia hamata*) was collected in central Texas at the Aransas National Wildlife Refuge (Fig. 2) in the San Antonio Bay system (Harper 1973, 1976). It occurred at only one of 11 stations and only once (December 1972) during ten months of sampling. No hydrographic data were taken at the site, but nearby bay water had temperature and salinity of 13°C and 14 ppt, respectively.

Three different investigators have collected *B. ligerica* in New Bayou, Brazoria County, Texas, upstream from its mouth at Chocolate Bay. S.M. Ray (unpublished) collected 31 specimens at 6 sites in June 1978. J.K. Fitzhugh and J.M. Nance (unpublished) collected a large number of specimens in February 1981 from a hard clay intertidal substrate; bottom water salinity and temperature were 2 ppt and 15°C, respectively. Nance (1984) subsequently (1980–81) sampled 17 silt-bottom sites monthly over an 18-month period but collected only 7 specimens.

In a sandy marsh area off West Bay, Galveston County, Texas, M. Emanuelsen (unpublished) has collected samples containing both *B. ligerica* and *B. hamata*. Analysis of these samples is incomplete, and abundance data are not available.

Thus, in Texas, *B. ligerica* exhibits patchy distribution with an apparent preference for a hard-clay substrate. These factors, along with its small size and similarity to *B. hamata*, have resulted in the species not having been reported previously.

ACKNOWLEDGMENTS

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THE DISTRIBUTIONAL HISTORY AND ECOLOGY OF MANGROVE VEGETATION ALONG THE NORTHERN GULF OF MEXICO COASTAL REGION

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ABSTRACT

Historical records and geologic evidence indicate that mangrove populations of the northern Gulf of Mexico region have varied considerably in abundance and species composition since at least the early Tertiary, principally as the result of global, regional and local climatic fluctuations. Recent isozymal and temperature tolerance research has revealed genetic variation between eastern and western Gulf and Caribbean populations of black mangrove and latitudinal ecotypic variations suggesting that an apparent Pleistocene extirpation of mangroves from the northern Gulf region may have caused genetic isolation of east-west populations and a mechanism for natural selection of latitudinal adaptive gradients during post-Pleistocene recolonization. The black mangroves of the coast of Texas have in the last century experienced populational declines and expansions primarily due to localized climatic extremes. During the last decade, black mangrove populations have rapidly expanded in Texas as a result of generally mild, mesic climatic conditions. However, in December of 1983, an extended period of extreme subfreezing temperatures caused an estimated 80 to 85 percent mortality in Texas mangrove populations. The surviving plants, from Galveston to the Rio Grande, in 1985 consist of very low stature individuals comprised mostly of recently (1984) germinated propagules and a few remnant, basally-sprouted older plants.

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INTRODUCTION

The present and past distribution and relative abundance of mangrove vegetation along the northern Gulf of Mexico coast is related in large part to a combination of habitat suitability, climatic conditions and genetic selection. At the present time, four principal mangrove species occur in the Gulf of Mexico. Red mangrove (*Rhizophora mangle* L.), white mangrove (*Lagun-*

cularia racemosa (L.) Gaertn.), black mangrove (*Avicennia germinans* (L.) L.) and button mangrove (*Conocarpus erectus* L.) occur northward along the coast of Mexico to La Pesca, Tamaulipas (Lot-Helgueras, Vasquez-Yanes and Menendez 1975, McMillan, unpublished data 1975–1976) and along the southern Florida Gulf coast as far north as Cedar Key (Davis 1940, Lugo and Zucca 1977), but only black mangrove occurs at locations along the northern gulf coast in Texas, Louisiana, and the extreme northern coast of Florida (Johnston, S.A., personal communication, 1981) at Ile de Chien, west of Apalachee Bay (Fig. 1). The three species other than *Avicennia* are limited to

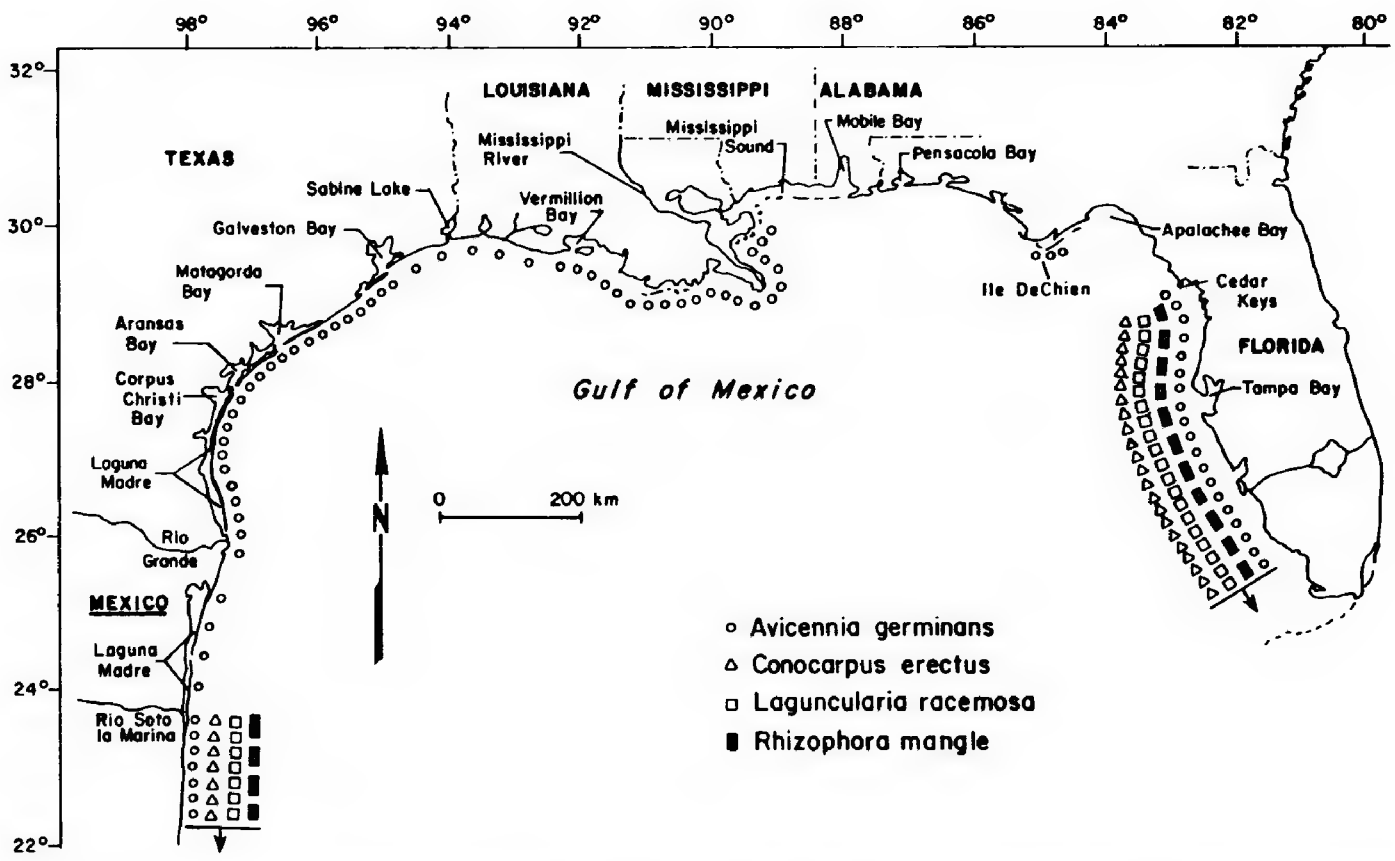

FIG. 1. Distribution of principal mangrove species along the northern coasts of the Gulf of Mexico.

the more tropical distribution in Mexico due to a lack of tolerance of chilling temperatures (Markley, McMillan and Thompson 1982). These species extend to a higher latitude along the Florida coast primarily as a result of the moderating effects of the Gulf on continental cold air masses which typically sweep into the Gulf from the northwest and move eastward to southeastward across the coastal region. Viable red mangrove propagules of northern Mexico origin frequently wash ashore along the Texas coast, but natural establishment has not been observed (McMillan 1971, Gunn and Dennis 1973, Markley *et al.* 1982). While black mangrove is local but abundant along the Texas coast (Sherrod and McMillan 1981), it is reported only as scattered and infrequent along the northern coast of Mexico between La Pesca and the Rio Grande (Rio Bravo Del Norte) (Lot-Helgueras *et al.* 1975). This is the

result of a lack of suitable mangrove habitat in northern Mexico. The apparent paucity of black mangroves between Galveston Bay, Texas and Vermilion Bay, Louisiana is for similar reason. The coastal region between Louisiana and northern Florida represents the most northern latitudes in the Gulf of Mexico. While suitable habitat occurs throughout much of this area, and black mangrove propagules arrive in beach drift on the islands of Mississippi Sound, mangroves are absent (Eleuterius, L.N., personal communication 1983) due to greater frequency and severity of cold winter conditions.

This paper traces the distributional history of mangroves in the northern Gulf region through their geologic and written records and evaluates past and present habitats and ecological requirements of these plants to allow a more accurate prediction of their distribution and abundance through time. Additionally, some light is shed on the possible causal agents and time frames behind the development of the latitudinal and east-west genetic variations in black mangrove populations of the Gulf and Caribbean.

DISTRIBUTIONAL HISTORY

Mangrove-like vegetation has had an almost continuous existence on the North American continent since the middle Paleozoic Era, approximately 350 million years ago, with only a few exceptions. Although the geologic record of mangroves in the northern Gulf region is not abundant nor continuous through time, the records that are available aid in the determination of the prehistoric distribution of these plants.

Krasilov (1975) stated that stems of plants, apparently of mangal type, were found in Devonian delta sediments in the eastern United States. Fossilized root structures discovered in Paleozoic and Mesozoic North American coal deposits bear very close similarities to present day mangrove rhizomes and pneumatophores (Cridland 1964). Cridland (*op. cit.*) speculated that these ancient plants of the genus *Amyleon* may have had the same growth form and occupied the same habitat that *Rhizophora* does today.

Darah (1939) mentioned the discovery of a possible progenitor of present day *Conocarpus* from Cretaceous deposits (approximately 100 million years ago) in Alabama.

The Eocene Epoch of the Tertiary (approximately 45 million years ago) is well represented in fossil plant remains throughout the southeastern United States. Probable ancestral forms of all the New World mangrove genera, except *Pelliciera*, have been reported from the northern Gulf region. Berry (1916) described two forms of *Avicennia* and a form of *Laguncularia* from the early Eocene in Tennessee and Mississippi. Another form of *Laguncularia* from more recent Eocene deposits in Alabama (Berry 1924) and Texas (Ball 1931) was considered by Berry (1924) to be an intermediate evolutionary form between the earlier and present day *Laguncularia*. *Conocarpus eoligniticus* Berry was described from early Eocene deposits in

Tennessee and Louisiana (Berry 1916) while *C. eocenicus* Berry was described from middle and late Eocene deposits in Alabama, Georgia, Louisiana and Texas (Berry 1924, Ball 1931). A form of *Rhizophora* has been found in late Eocene deposits in Georgia and possibly from Mississippi (Berry 1924). The fern genus *Acrostichum*, which is frequently associated with present day mangroves in Florida and Mexico, also has representatives in the Eocene with fossils collected in Georgia, Alabama, Mississippi and Louisiana (Berry 1924). Berry (1916, 1924) stated that the Eocene mangrove swamps of the southeastern U.S. were probably very similar in structure and composition to the present day mangals of southern Florida, Mexico and tropical America.

There is a lack of mangrove fossil evidence from North America following the Eocene until approximately 3000–4000 years ago. However, *Avicennia* was recorded from the Miocene and Pliocene of Trinidad (Darah 1939) as well as from the Pleistocene in Trinidad and Panama along with *Rhizophora* (Berry 1924, 1925, Bartlett and Barghoorn 1973). The lack of fossil records in the northern Gulf region during these periods suggests that mangroves were eradicated from that area by the progressively cooler climatic conditions immediately preceding and into the Pleistocene and were restricted to more equatorial localities in the Caribbean.

Recent sedimentary record of mangroves in Texas apparently has not been investigated. However, Davis (1940) and Scholl (1964) recorded Holocene mangrove peat deposits along the present coast of Florida dating from 3000–4000 years ago up to present time.

Written accounts of mangroves in the Gulf and Caribbean date to the early 1500's with reports from Florida, Mississippi and Louisiana throughout the 1700's and 1800's (Chapman 1975, Moldenke 1960). The earliest record of black mangrove in Texas was an 1853 collection from the mouth of the Rio Grande (Sherrod and McMillan 1981). *Avicennia* was reported from Tamaulipas, Mexico, during the early 1900's by Conzatti and Smith (1910). While the 1853 collection remains the only direct evidence of black mangroves in Texas before the 1930's, when they began appearing regularly in herbarium collections and written records, indirect evidence strongly suggests that *Avicennia* has been present in Texas for hundreds or perhaps thousands of years following the end of the Pleistocene. Within this century, collections and observations have indicated that the overall distribution of black mangrove in Texas and the northern Gulf has expanded and contracted in response to variations in environmental conditions (Sherrod and McMillan 1981).

DISTRIBUTIONAL ECOLOGY

Mangroves, being primarily of tropical distribution, fringe on the border of their range along the northern coasts of the Gulf of Mexico. Temperature, salinity, and various other environmental factors have been shown to affect the establishment and survival of *Avicennia* in this area.

Low winter temperature is one factor which significantly influences the distribution of mangroves. Laboratory experiments have indicated that mangrove populations of the Gulf of Mexico and Caribbean exhibit gradients in their ability to tolerate chilling temperatures (2–4°C) which are correlated with latitudinal origin of the plants, pointing to a natural selection process which has resulted in adaptive genetic differentiation (McMillan 1975a, Markley *et al.* 1982). Black mangroves from central and southern Texas were able to withstand exposures to chilling temperatures which produced considerable plant damage to plants of the same species from more tropical locations in Mexico. Plants from extreme southern Mexico and other Caribbean locations exhibited the greatest damage from exposure to chilling temperatures while those plants from the central Mexican coast showed intermediate effects. Plants of Florida were more tolerant of chilling temperatures than were plants of Jamaica and St. Croix. All plants were cultured under uniform laboratory or greenhouse conditions for several years prior to the chill tolerance experiments. The same adaptive latitudinal gradients have been demonstrated in similarly distributed species of tropical seagrasses in the Gulf of Mexico and Caribbean (McMillan 1979, McMillan and Phillips 1979).

Freezing temperatures, as are occasionally experienced along the Texas coast, can produce aboveground damage or mortality in Texas plants, as evidenced during certain previous winters. In December 1983, the Texas coast experienced one of the most severe, extended periods of low winter temperatures in recent history. Sub-freezing temperatures prevailed during a 9-day period with extremes plummeting to the −6° to −10°C degree range on several occasions during that period (NOAA 1983). Extensive damage to ornamental, cultivated, and native plants of tropical distribution occurred, including mangrove populations. Preliminary quantitative sampling of mangroves in the vicinity of Harbor Island, Texas, in May 1984, indicated that 85 percent of the mangroves in that area were lost (Sherrod, unpublished data 1984). Other qualitative observations along the Texas coast in 1984 revealed probable mortalities ranging from 95+ percent at Galveston Island to perhaps 60 or 70 percent on the lower coast near Brownsville. Surviving plants were either very low in stature (generally with a single stem less than 0.3 m in height) or were resprouting from the base of multiple-stem plants at heights usually less than 0.5 m above the ground. Many propagules which were thermally protected from the sub-freezing temperatures by ice coating or dense vegetation or debris coverage also survived the freezing temperatures and successfully established in 1984. Photographs taken in April and May, 1985 (Figs. 2 and 3) show the typical mortality and slow recovery of the mangrove populations on the south Texas coast. Similar freeze effects have been noted in Florida (Davis 1940, Lugo and Zucca 1977) and in Louisiana (West 1977). The frequency, duration, and/or severity of freezing temperatures is a prime factor governing the distribution and abundance of black mangroves in the extreme northern Gulf.

FIG. 2. Black mangroves on Harbor Island, Texas in April 1985 depicting typical mortality following the December 1983 freeze. Center plant in foreground has resprouted at base. An approximate 80–85 percent mortality was realized in this area.

FIG. 3. Recently established (1984) seedlings and basally resprouting plants typify 1985 mangrove populations in Texas. As is apparent in the background of this May, 1985 photograph from South Padre Island, Texas, survival rates following the 1983 freeze were higher (50–60 percent) on the extreme south Texas coast than in more northern localities.

Droughts and associated hypersaline conditions may also govern mangrove distribution and abundance. *Avicennia* is generally quite tolerant to broad changes in salinity and can survive hypersaline conditions (100 to 180 ppt.) for several days (McMillan 1974). However, many coastal areas of south Texas and northern Mexico may experience hypersaline conditions greater than or equal to these extremes for weeks or months during extended droughts as experienced during the 1950's, especially in areas that are not located near passes to the open Gulf. Mangroves can become locally confined to areas of direct influence by moderating Gulf waters during extended drought periods (McMillan 1975b), but expand their distribution to peripheral areas during periods of higher rainfall.

Another environmental factor which may affect the distribution of *Avicennia* in the northern Gulf relates to habitat suitability for seedling establishment. McMillan (1971) concluded that low-energy, shallow-water environments were necessary for the establishment of black mangrove seedlings in Texas. Hypocotyl and root development were greatly inhibited in seedlings exposed to water turbulence under laboratory conditions and establishment of seedlings was increasingly inhibited in water depths exceeding 5 cm. The three areas of major mangrove concentration in Texas (Sherrod and McMillan 1981) all are of similar physical characteristics, being low relief islands or shorelines just inside major passes through the barrier islands with significant bodies of water on their northern boundary. These habitats are the most stable for mangrove existence through time, providing low-energy, shallow water sites with moderated salinities and a slight thermal barrier to cold winter temperatures provided by the north flanking embayments.

CONCLUSIONS

Prior to the Pleistocene Epoch, world climate was fairly moderate and consistent for millions of years (Brooks 1970). Fossil evidence indicates that mangroves and other tropical plant species probably existed profusely throughout this time in what is now North America. However, broad, but gradual fluctuations of sea level and tectonic movements produced different coastlines from what are present today. Figure 4 indicates the probable distribution of mangrove vegetation in the Caribbean and Gulf of Mexico prior to the Pleistocene based on Eocene fossil records.

The Pleistocene Epoch was characterized by alternating glacial and interglacial periods. Immediately preceding the Pleistocene and during the successive glacial periods of that epoch, regional climate cooled well below the tolerance of mangroves and other tropical species in the northern Gulf and they were probably eradicated from that region, as is suggested by the lack of fossil evidence. Pleistocene fossil evidence from the southern Caribbean indicates that mangroves were more equatorially restricted during that epoch (Fig. 5). However, during the alternating interglacial

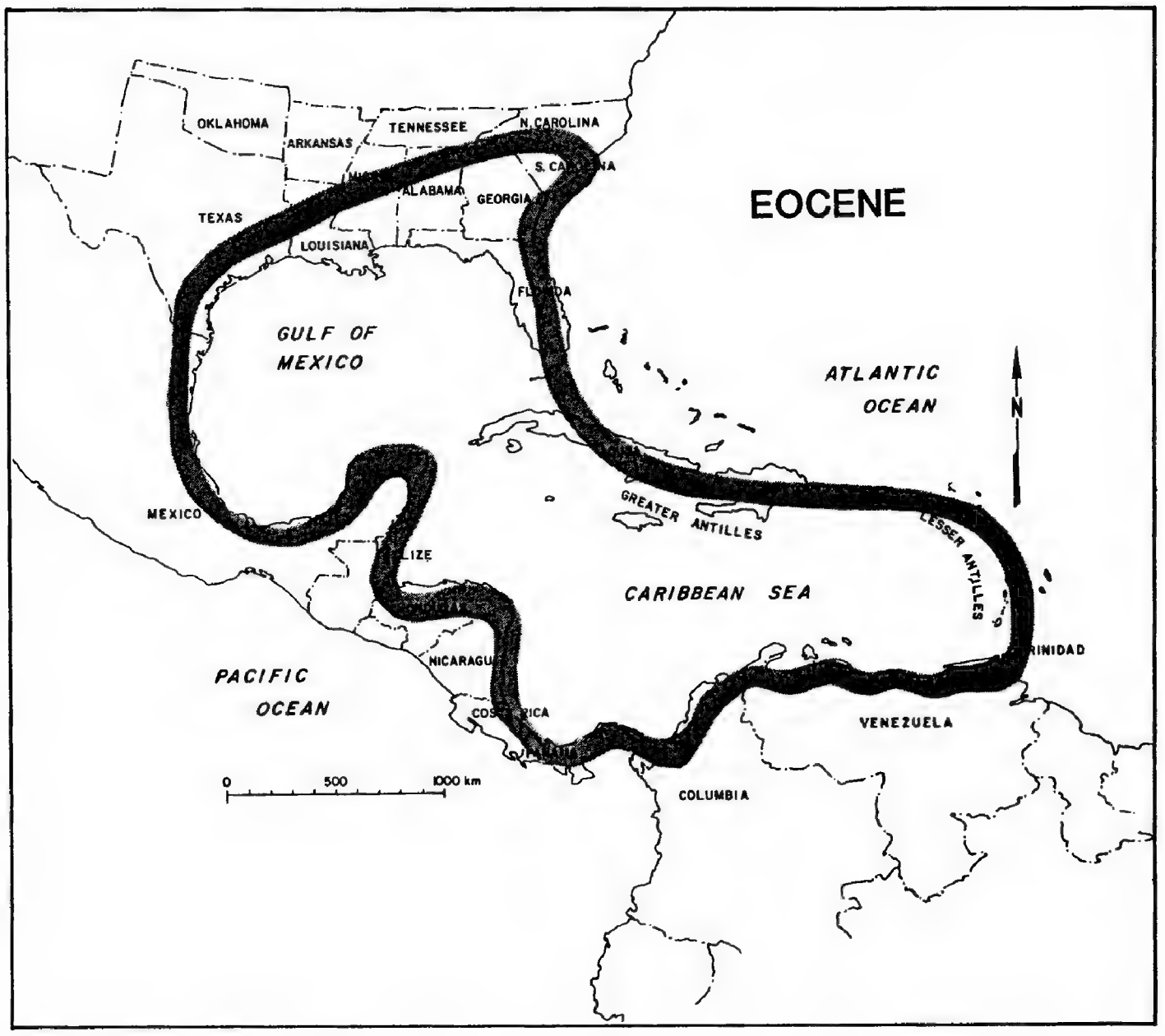

FIG. 4. Probable mangrove distribution prior to the Pleistocene, as indicated by Eocene fossil evidence.

periods of the Pleistocene, regional climate may have moderated sufficiently to allow temporal migration of mangrove populations from the more tropical locations. This alternating retreat and advance of mangroves in response to the dramatic changes in regional climate may have been the mechanism for the development of chill tolerant populations of black mangroves through natural selection.

Approximately 3000–4000 years ago, present day marsh environments along the Texas coast began forming (McGowen and Brewton 1975). Barrier islands developed and with their formation came the shallow, low-energy environments favorable for mangrove reestablishment. As regional climate gradually warmed, recolonization of the northern Gulf by mangroves began with natural selection allowing the more chill tolerant strains to progress further northward, resulting in the latitudinal gradient of chill tolerant populations observed today (Fig. 6).

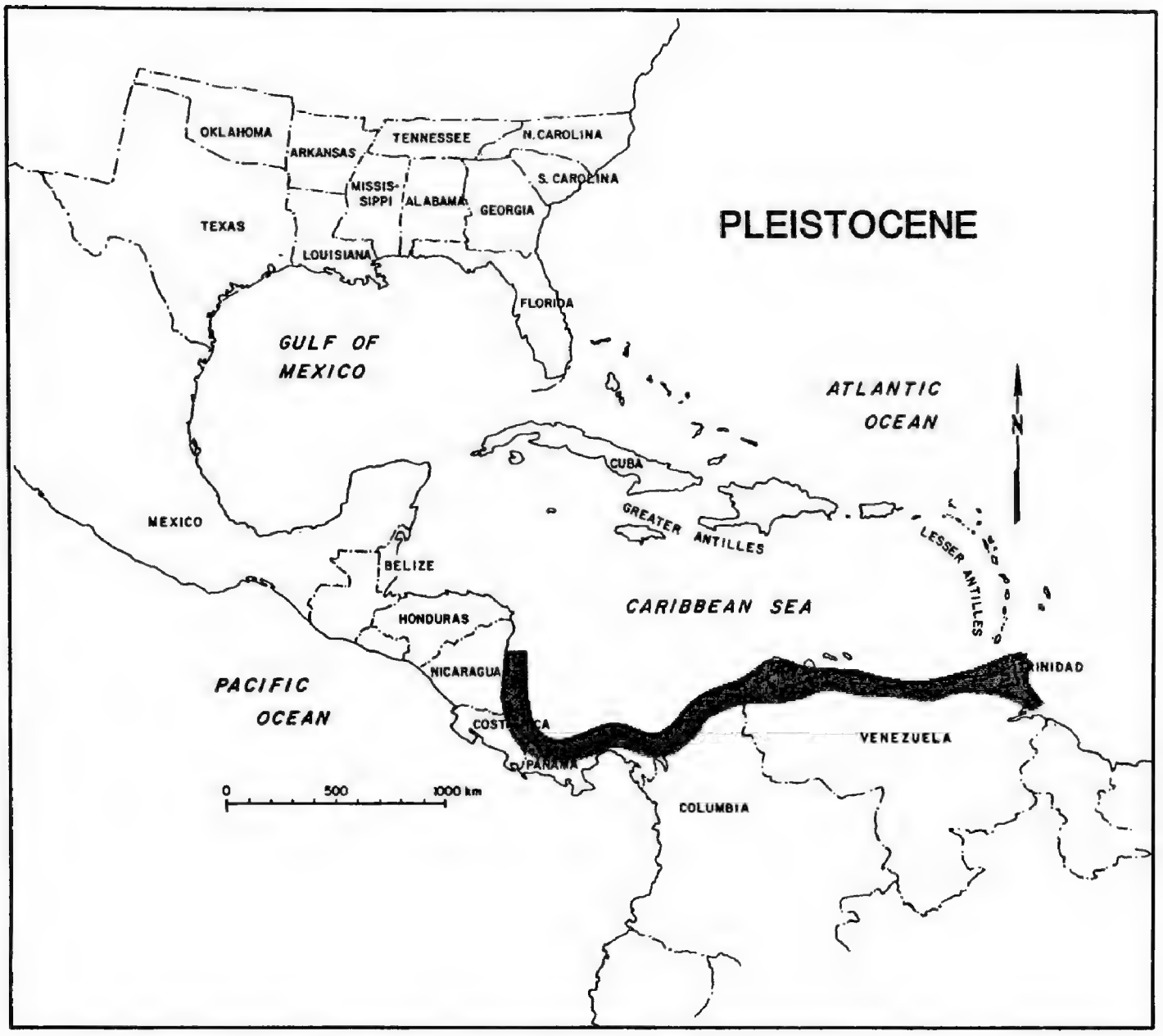

FIG. 5. Probable mangrove distribution during the Pleistocene, as indicated by fossil evidence of that epoch.

In addition to latitudinal genetic variation, populations of black mangroves from the eastern and western Gulf and Caribbean have been shown to exhibit different isozyme patterns (McMillan, unpublished data, 1979–84) indicating genetic isolation and bilateral evolutionary divergence. Plants from Florida and the eastern Caribbean show similar isozyme patterns while plants from Texas and Mexico exhibit a different pattern. Plants from the western Caribbean (Belize, Panama) show a mixture of patterns possibly as a result of mixing oceanic currents facilitating genetic communication in that region. The apparent eradication of mangrove vegetation from the northern Gulf during the Pleistocene and subsequent recolonization since that time may have provided the mechanism for the development of the latitudinal and longitudinal intraspecific genetic variations in black mangrove populations. As mangrove vegetation recolonized the Gulf of Mexico from sources in the Caribbean, separate prevailing northward currents

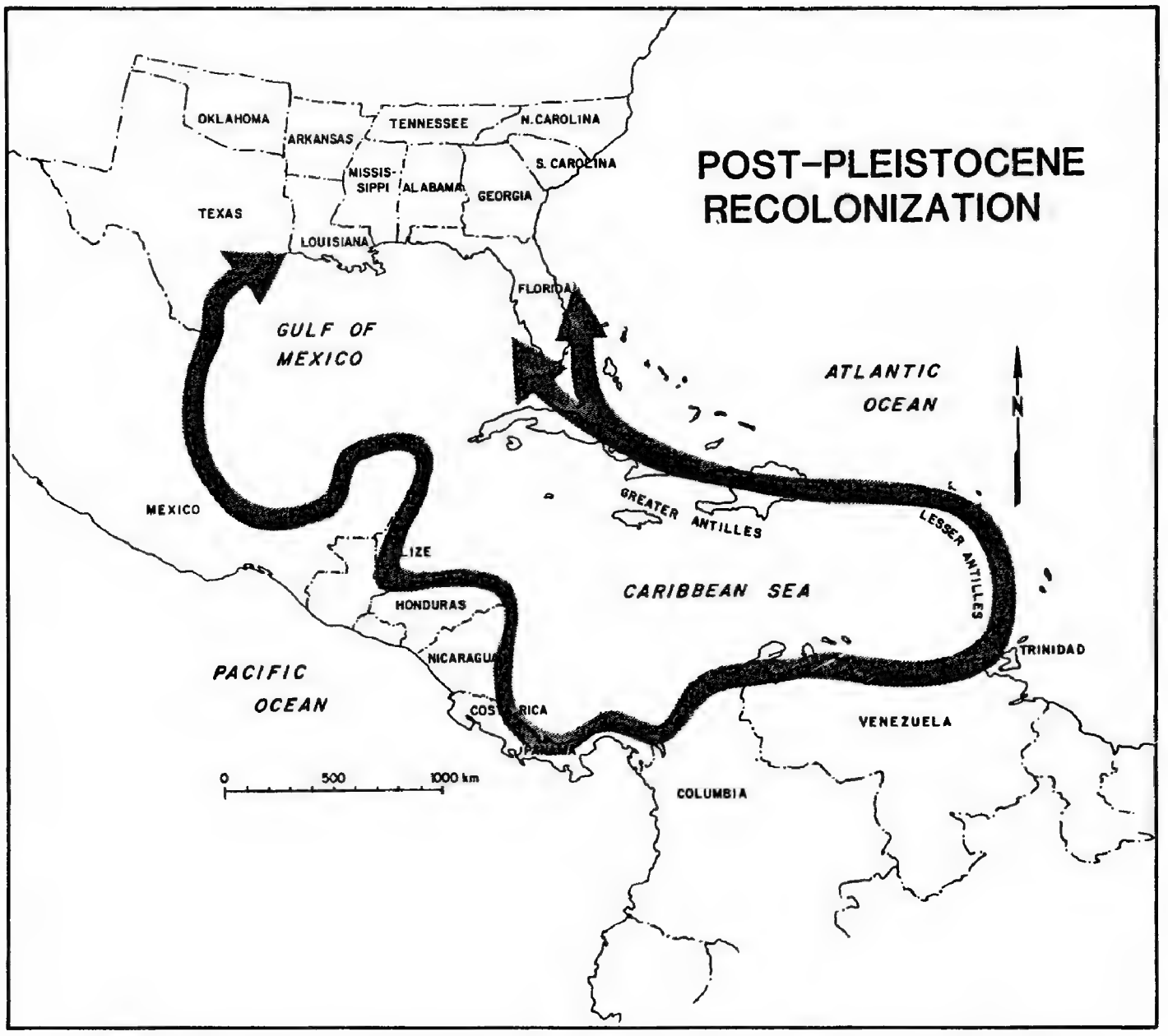

FIG. 6. Post-Pleistocene recolonization of mangroves into the northern Gulf of Mexico.

along the eastern and western Gulf would have maintained the segregation of east and west populations resulting in bilateral evolutionary divergence.

During the last two centuries several periods of extreme cold and drought have occurred along the Texas coast which could explain the apparent fluctuations in recent mangrove distribution and abundance. Additionally, within this century numerous coastal land form modifications as a result of natural processes and human activity have been demonstrated to result in localized increases and decreases in intertidal marsh habitats along the Texas coast (McGowen and Brewton 1975, White, Morton, Kerr, Kuenzi and Brogden 1978), thus also contributing to recent mangrove fluctuations. During the last two decades until 1983, moderate local climatic conditions and increased environmental awareness and management allowed mangroves to rapidly expand their distribution and relative abundance in Texas. The December 1983 freeze resulted in an 80–85 percent reduction in Texas mangrove populations. A population recovery in Texas to the extent present in the early 1980's could require 10, 20 or more years depending on local climatic conditions and coastal management policies in the future.

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THE SEED RESERVE FOR *HALODULE WRIGHTII*, *SYRINGODIUM FILIFORME* AND *RUPPIA MARITIMA* IN LAGUNA MADRE, TEXAS

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ABSTRACT

For the submerged marine macrophytes that occur in bays and estuaries of the Texas coast, seed reserves for *Halodule wrightii* Aschers. and *Ruppia maritima* L. were widely distributed in sediments in both Upper and Lower Laguna Madre (26°–27° 40′ N, lat.), but those for *Syringodium filiforme* Kütz. were recorded only in the Lower Laguna Madre with the highest incidence in the southernmost portion. Fruits and/or fruit fragments of at least one of the three species were found in 79% of the sediment samples. The highest number of one-seeded fruits for *H. wrightii* was recorded as 1154 m^{-2}, for *S. filiforme*, 1642 m^{-2}, and *R. maritima*, 4110 nm^{-2}. The recent changes in the composition of the vegetation of the Lower Laguna Madre, with *Syringodium* invading areas previously recorded with only *Halodule*, probably reflect an active role for the seed reserves of marine macrophytes.

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INTRODUCTION

Although seed reserves have been evaluated for diverse land areas (Harper 1977, Roberts 1981, Archibold 1981, Keddy and Reznicek 1982, Holthuijzen and Boerboom 1982, among others), those for aquatic ecosystems have not received wide attention. Prairie glacial marshes have been evaluated for seed reserves by Van der Valk and Davis (1976, 1978, 1979) and a freshwater tidal wetland was examined by Leek and Graveline (1979). The emergence of seedlings from lake sediments has been studied by Haag (1983) and the seed reserve in a California salt marsh has been investigated by Hopkins and Parker (1984). The seed reserves for submerged marine macrophytes only recently have received attention.

For the marine macrophytes that produce dormant seed, studies have been conducted into the buried seed populations of *Zostera*, *Halodule*, *Syringodium*, *Cymodocea* and *Ruppia*. Bigley (1981) studied the germination of *Zostera japonica* Aschers. & Graebn. and *Ruppia maritima* L. from the seed reserve in an intertidal delta in the Strait of Georgia, British Columbia. McMillan (1981) examined the status of seed reserves for *Halodule wrightii*

Aschers. and *Syringodium filiforme* Kütz. in the Western Atlantic. McMillan, Bridges, Kock, and Falanruw (1982) studied the seed reserve for *Cymodocea rotundata* Ehrenb. & Hempr. on the coral shelves of Yap, Micronesia. Two other genera that produce dormant seeds, *Heterozostera* and *Halophila* (den Hartog 1970), also may have seed reserves in marine sediments.

The one-seeded fruits of the three species in *Halodule*, *Syringodium* and *Ruppia* in Texas have distinctive properties. Those of *Halodule* are round and black, ranging from *ca.* 2.0 to 2.7 mm in diameter (McMillan 1981). Those of *Syringodium* are flattened, tapering in two directions, and tan to brown, ranging from 4.8 to 7.4 mm in length (McMillan 1981). The fruits of *Ruppia* are the smallest, *ca.* 1.5 mm in diameter and black with a tapering point, occasionally with the pedicel still attached. Although dormant seeds of *Halophila engelmanni* Aschers. may have been present in the sediment samples, their small size precluded their being identified without microscopic inspection. For *Halodule*, fruits mature at rhizome level and may remain in the seed reserve under the pistillate plants until they germinate or are transported elsewhere through sediment disturbance. In both *Syringodium* and *Ruppia*, a genus which occurs in both marine and brackish waters, the fruits are produced on stems above the sediment surface and are likely to be widely disseminated upon maturity.

The sediment samples that were examined in the present study of seed reserves were part of an intensive investigation of Laguna Madre conducted by the Bureau of Economic Geology of The University of Texas at Austin. The sampling covered the full extent of the hypersaline bay, *ca.* 150 km along the southern coast of Texas. This study of seed reserves for marine macrophytes represents a first assessment in a large coastal embayment that has shown recent changes (Singleton 1964, McMahan 1965, Merkord 1978) in the composition of the seagrass vegetation.

MATERIALS AND METHODS

The seed reserves were examined in 18 sediment samples from Upper Laguna Madre and 50 from Lower Laguna Madre. The 68 samples were selected from 143 that had been released by the Bureau of Economic Geology and had been examined previously for other biological and geological information. Most samples had field notes indicating that they had been collected in or near seagrass beds: 10 had *Syringodium* in the vicinity, 28 had *Halodule* and 7 had *Ruppia*. In addition, *Halophila engelmanni* was noted in 7 sample sites (4 with *Halodule* and 1 with *Syringodium*) and *Thalassia testudinum* Banks ex König at 4 sample sites (1 with *Halodule*). For 19 samples, no seagrasses were noted on the field data sheets.

The location of 398 (L) samples on a 1-mile grid and 331 (JM) samples on a 0.5-mile grid (adjacent to Arroyo Colorado Cutoff, 26° 30′–26° 15′) is indicated on three sheets of the Submerged Lands of Texas (Fisher 1978): Corpus Christi Sheet, Kingsville Sheet and Brownsville-Harlingen Sheet. The samples used in this study from the longer grid included: L14,17,18,21,23,28,29,55,60,64,66,71,75,81A,116,125,130,137,140,141,145,158,174,185,187,190,191, 202,205,214,217,226,227,307,312,313,320,327,328,353,372,374,377A,379,388,390,392,393,395, and those on the shorter grid were: JM2–8,10.5,11,68,70,153,156,181,183,236,238,241.

The samples were placed into 10% formalin at the time of collection in 1977 and later transferred to 70% ethanol for storage. Most samples represented the sediment obtained with a

single drop of a grab sampler with an opening of 15 cm^2, but a few with coarse texture were obtained with a shovel. The samples were stored in sealed glass bottles.

Because of the volume of sediment that had to be sorted by hand, the 68 samples were initially screened by biology classes at Crockett High School in Austin as part of a project that was conducted in conjunction with the Science Education Center of The University of Texas. Although the students were given a week of intensive study of marine macrophytes and provided with samples of fruits of each of the three species, a reliability check that was conducted on 10 samples indicated that many fruits had been overlooked or misidentified in the initial screening. For the final assessment, all of the samples were re-examined by one observer.

RESULTS

The fruits of the submerged marine macrophytes were widely distributed in the sediments of Laguna Madre. Fruits and/or fruit wall fragments were recorded in 79% of the sediment samples. Among the samples without fruits, eight were among the 18 from Upper Laguna Madre and five were among the 50 from Lower Laguna Madre (Table 1).

TABLE 1

Number of Sediment Samples with Fruits of Submerged Macrophytes[1]

Kind of fruit[2]	Number in Upper Laguna Madre		Number in Lower Laguna Madre			Total
	N	S	N	C	S	
Ruppia	2		2			4
Halodule	3	1	3	5	4	16
Syringodium			1		1	2
Ruppia/Halodule	4	1	5	12	1	23
Halodule/Syringodium					8	8
Ruppia/Halodule/ Syringodium			1	1	1	3
No fruits (or fragments)	7		4		1	12
Number of sediment samples	16	2	16	18	16	68

[1] Samples L14 through L116 were in the northern part (N) of Upper Laguna Madre; L125 and L130 were in the southern part (S) (the hole); L137 through L227 were in the northern part (N) of Lower Laguna Madre; JM2 through JM241 were in the central part (C) and L307 through L395 were in the southern part (S). A complete list of the sediment samples is given in Materials and Methods.

[2] Whole fruits as well as fruit fragments are included in the census.

The most widely distributed fruits were those of *Halodule.* These fruits or fruit wall halves were recorded in 75% of the samples. *Ruppia* fruits were recorded in 44% of the samples and *Syringodium* fruits were noted in 19% of the samples. Although *Halodule* and *Ruppia* fruits were recorded throughout Laguna Madre, those of *Syringodium* were found only in Lower Laguna Madre (Fig. 1).

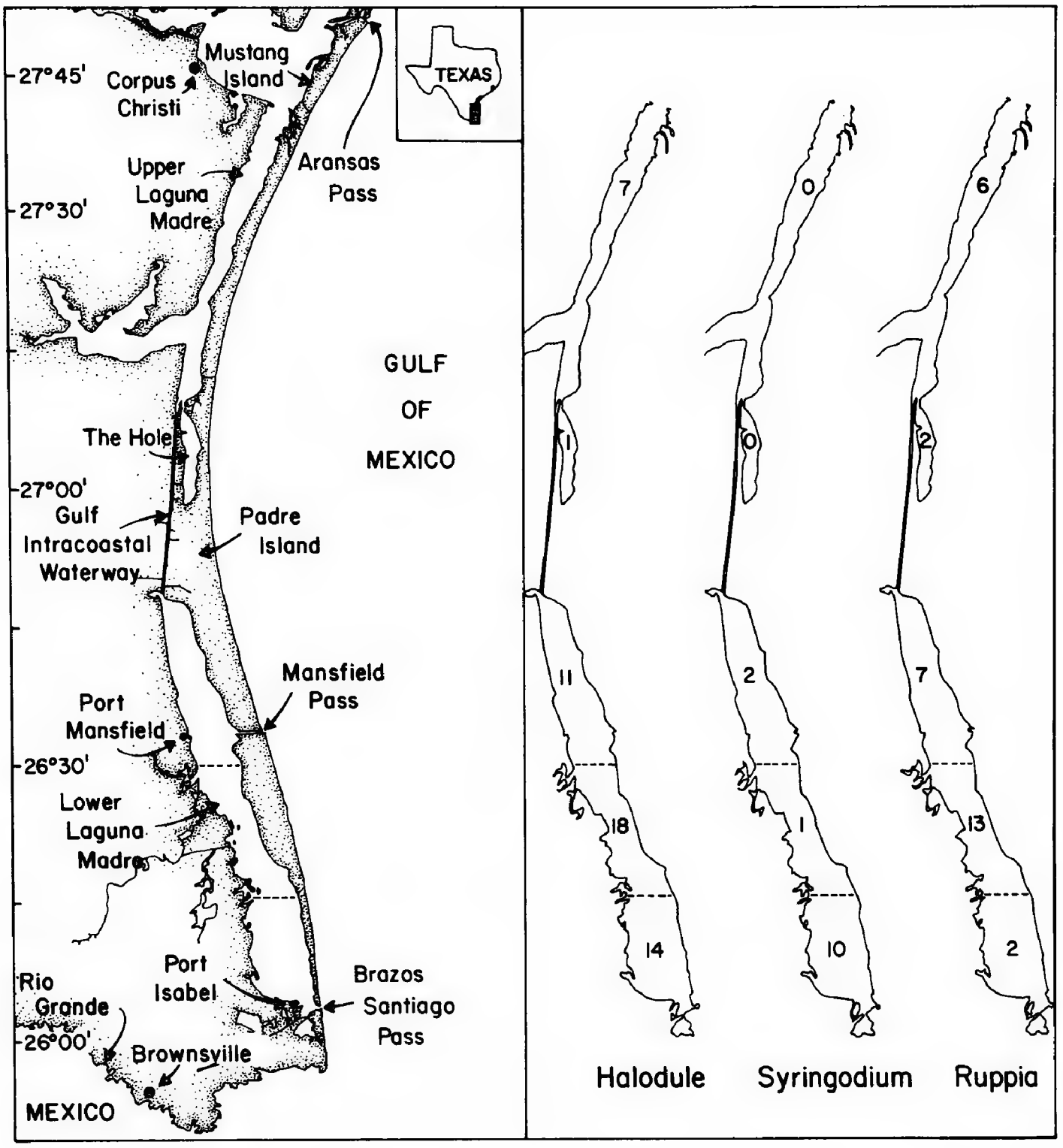

FIG. 1. Maps of Laguna Madre showing number of sediment samples that contained fruits of three marine macrophytes: *Halodule wrightii*, *Syringodium filiforme* and *Ruppia maritima*. The total number of sediment samples examined were: Upper Laguna Madre, northern, 16; the Hole, 2; Lower Laguna Madre, northern, 16; central, 18; southern, 16.

Although seeds of *Halophila* and *Thalassia* were not included in the study, those of *Halophila* being very small, as indicated above, and those of *Thalassia* not remaining dormant, the reserves for the other macrophytes were recorded in areas where *Halophila* and *Thalassia* occurred (Table 2). In the four samples collected in *Thalassia* beds, fruits of *Halodule* and *Syringodium* were found in three of them. Among seven samples collected in areas with *Halophila*, fruits of *Halodule* occurred in two.

TABLE 2

Occurrences of Fruits of Submerged Macrophytes in Laguna Madre[1]

Kinds of fruits[2]	Number of sediment samples containing fruits in sites with various combinations of macrophytes									
	R	H	H/HP[3]	H/T[4]	T[4]	HP[3]	S	S/H	S/HP[3]	None Reported
Ruppia (R)		1	1							2
Halodule (H)	2	5				2	2	1		5
Syringodium (S)		1			1					
Ruppia/Halodule	5	10	1				2			5
Halodule/Syringodium		1			2		3			1
Ruppia/Halodule/ Syringodium		1								2
No fruits		3	2	1			1		1	4
Total number of sediment samples	7	22	4	1	3	2	8	1	1	19

[1] Field notes recorded at the time of the sediment collections indicated that various combinations of macrophytes occurred at the sampling site. No macrophytes were listed for 19 collections.
[2] Occurrences of whole fruits as well as fruit fragments are included in the census.
[3] HP = Halophila
[4] T = Thalassia

Among 10 samples that were examined from areas with *Syringodium* (Table 2), three contained at least one *Syringodium* fruit or fragment. Eight of the 10 samples contained fruit or fruit wall halves of *Halodule*, but the number of intact fruits was small, 3–6, and the number of wall halves ranged in four samples between 18 and 22.

The maximum seed reserves are included in Table 3. For *Halodule*, a

TABLE 3

Number of Macrophyte Fruits in Sediment Samples from Laguna Madre[1]

	Number of sediment samples containing									
	1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100 fruits
Ruppia	22	4	1		1	1				1
Halodule	38	8	5							
Syringodium	11	1		1						

[1] Numbers include whole fruits and fragments. For Halodule, fruit wall halves were common in the sediment samples. Of the 51 samples with Halodule fruits, 21 contained whole fruits. The sample with the most fruits (26) contained only whole fruits. For Syringodium, the sample with the highest number (37) contained only whole fruits. The highest number of whole fruits of Ruppia was 93.

sediment sample from the lower part of the Lower Laguna Madre (L328) contained 1154 m^{-2} (whole fruits). Field notes for this seed population indicated that it was taken from a shallow seagrass bed adjacent to Padre Island and that *Halodule* was growing at the site. For *Syringodium*, the

maximum was 1643 m^{-2} (whole fruits) in a sediment sample (L372) toward the bay center of the lower part of the Lower Laguna Madre. The field notes for the seed population of *Syringodium* indicate that both *Syringodium* and *Halodule* were growing at the collection site. For *Ruppia*, the maximum was 4110 m^{-2} in a sediment sample (L116) at the lower part of the Upper Laguna Madre. The field notes indicate that this buried seed population for *Ruppia* was in a shallow bay margin and that both *Halodule* and *Halophila* were growing at the collection site. As indicated in Table 3, 75% of the seed populations of *Halodule*, 73% of those of *Ruppia* and 85% of those of *Syringodium* were 440 m^{-2} or less.

DISCUSSION

Although an initial investigation of seed reserves in Laguna Madre in 1977 indicated that *Halodule* fruits were common in sediments of the Port Mansfield area (McMillan 1981), the present survey shows a seed reserve throughout the Laguna Madre. The distribution of the seed reserves reflects the patterns of occurrence of the three macrophytes. *Halodule* and *Ruppia* occur throughout the Laguna Madre, but *Syringodium* is confined to the Lower Laguna Madre (J. Chin, personal communication 1977–1978; Merkord 1978; McMillan, unpublished data 1977–1984).

In areas with *S. filiforme* as the dominant or only macrophyte, fruits or fruit wall halves of *H. wrightii* occurred in the underlying bay sediments. In five of the eight sediment samples from areas with *Syringodium* as the dominant macrophyte, only *Halodule* fruit wall halves were noted, indicating no recent production of *Halodule* fruits and the possible colonization of a *Halodule* area by *Syringodium*. The sediment samples containing large seed reserves for *Syringodium* were from beds of *Halodule* or *Thalassia*, indicating the wide dispersal of fruit of this colonizing species.

Although the sediment samples had been preserved in alcohol which precluded a check for viability, studies of *Halodule* fruits that were obtained in Laguna Madre (McMillan 1981, 1983, unpublished data 1982–84) sediments at Padre Island have shown a seed germination percentage as high as 63 and have shown a continuous "time-capsule" type of germination for over 3 years. *Syringodium* fruits that were collected from infructescences in Laguna Madre also demonstrated a "time-capsule" type of seed germination as did fruits sieved from sediments at Key West, Florida, and at Jack's Bay, St. Croix (McMillan 1981).

Changes in the distribution of the aquatic macrophytes occurred in Laguna Madre during the 1960s and 1970s and may indicate an active role of a seed reserve. The maps prepared by J. Pipkin (personal communication 1961) during 1960–61 indicated that *S. filiforme* was restricted to Port Isabel Bay at the southern end of Lower Laguna Madre (Singleton 1964). A resurvey in 1964–65 showed significant increases in the distribution of *S. filiforme* with a northward extension into areas that were formerly dominated by *H. wrightii* (McMahan 1965). The surveys of 1974–75 (Merkord

1978) documented further northward extension of *S. filiforme* and indicated that it had become a dominant macrophyte as far north as southern Redfish Bay, in the vicinity of Port Mansfield (Fig. 1). Flowering plants of *S. filiforme* were common in the vicinity of Port Mansfield in 1977 and circular patches of *S. filiforme* in *Halodule* areas (McMillan, unpublished data 1977) may indicate that the rapid spread of *Syringodium* into *Halodule* areas was facilitated by seed production of *Syringodium.*

The changes in the distribution patterns of the aquatic macrophytes reflect environmental changes that have occurred in the Laguna Madre during the 1950s, 1960s and 1970s. The completion of the Gulf Intracoastal Waterway in 1948 provided an interchange of water between Upper and Lower Laguna Madre and reduced the hypersalinities that had been reported by Simmons (1957). The redredging and stabilizing of Mansfield Pass with jetties in 1962 formed a permanent opening to the Gulf of Mexico near the northern end of the Lower Laguna Madre. These changes coupled with the end of a prolonged drought (1951–1957) in Texas have resulted in a general reduction of hypersalinity conditions.

The recent invasion of *Halodule* areas by *Syringodium* may reflect their different tolerances for salinity and temperature. *Halodule* is the more tolerant of hypersaline conditions as shown by McMillan and Moseley (1967) and McMahan (1968). Recent studies of temperature tolerances (McMillan 1984) indicate that *Halodule* is also more tolerant of high temperature stresses. The lowering of the salinities in Laguna Madre during the 1960s promoted the wider distribution of *Syringodium*, but because of differences in heat tolerances, *Syringodium* is excluded from *Halodule* areas that are apt to be exposed to sustained high temperatures at low tides.

The seed reserves in marine areas have not been studied sufficiently to determine if those of the Laguna Madre of Texas are representative of seagrass areas in other parts of the world. Den Hartog (1970) had not examined sediments for seed reserves at the time of the publication of his monograph, *The Sea-grasses of the World*, and emphasized the vegetative reproduction of seagrasses. He reported that inflorescences, flowers, fruits and seeds "are not often found in most sea-grasses," but intensive investigations are now showing that seeds and fruits are more common than previously indicated.

Although the buried seed populations for the submerged marine macrophytes do not equal those of arable land which may contain *ca.* 30,000 to 157,000 seeds m^{-2} (Harper 1977), they are in the range reported for prairies and forests (Harper 1977). For *Halodule wrightii*, McMillan (1981) had reported a maximum of 3120 m^{-2} for Port Mansfield, Laguna Madre. Johnson and Williams (1982) reported a maximum of 3300 m^{-2} (including fruits of various stages of maturity) for *H. wrightii* at Jack's Bay, St. Croix. A seed reserve has been reported for *Halodule wrightii* in several bays in Florida, including Biscayne Bay and St. Joseph Bay, as well as in the Florida Keys (McMillan 1981) and has recently been observed for *H. uninervis* (Forsk.) in another hypersaline bay, Shark Bay, Western Australia (McMil-

lan, unpublished data 1981). McMillan (1981) examined numerous sediments in the Western Atlantic, but found fruits of *Syringodium filiforme* only at the base of a pistillate plant at each of two sites, Key West, Florida, and Jack's Bay, St. Croix. In addition, a few fruits of *S. filiforme* were recovered from sediment cores that were examined on Buck Island, St. Croix (McMillan, unpublished data 1977), but the fruits of *S. filiforme* may be underreported in the reserves because of their resemblance to shell fragments.

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STAMINATE FLOWERS AND REPRODUCTIVE PHYSIOLOGY OF *HALOPHILA ENGELMANNI*

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ABSTRACT

Field observations and studies under controlled conditions at intervals from 1972 to 1985 indicate that the reproductive physiology of *Halophila engelmanni* Aschers., a common seagrass in the Gulf of Mexico, is primarily under temperature controls. Staminate flowers that were observed for the first time in Redfish Bay, Texas, in 1972 were observed in late April to mid-June in subsequent years and produced in the laboratory at any time of the year under temperatures between 22 and 27.5°C and day lengths longer than 12-h. Pistillate flowers were more consistently produced over an extended period of time. Flowers were produced under the inductive temperatures and continuous light, as is also characteristic of other tropical seagrasses, indicating that temperature plays a major role in the phenological timing of reproductive activity of *H. engelmanni*.

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INTRODUCTION

Among the species in *Halophila* section *Halophila*, *H. engelmanni* Aschers. had no description of staminate flowers at the time of publication of *The Sea-Grasses of the World* by C. den Hartog (1970). Staminate flowers were reported in Redfish Bay, Texas, and in laboratory cultures (McMillan 1974) and were described for the first time by McMillan (1976). Recently, staminate flowers were reported in Indian River, Florida, by Short and Cambridge (1984). In section *Halophila*, staminate flowers are still unreported for *H. johnsonii* Eiseman which also occurs in the Indian River of Florida (Eiseman and McMillan 1980), but have been observed recently for *H. hawaiiana* Doty & Stone (D. Herbert, personal communication, 1985).

Although both field observations and laboratory cultures for 1973–74 were reported briefly for *H. engelmanni* by McMillan (1976), subsequent studies at intervals through 1985 have added further insight into the status of staminate flowers and the phenological timing of reproductive activity. The recent observations of staminate flowers in Florida by Short and Cambridge (1984) differ in some respects from those reported earlier in Texas by McMillan (1974, 1976) and have raised questions concerning the roles of

temperature and photoperiod in the reproductive physiology of *H. engelmanni.*

MATERIALS AND METHODS

The primary study site has been in Redfish Bay on the shallow margins of Stedman Island and other dredge spoil islands along the causeway between the cities of Aransas Pass and Port Aransas (Wiginton and McMillan 1979). Phenological observations that were recorded at monthly intervals from November 1973 through September 1974 (McMillan 1976) have been continued at intervals to May 1985. Additional observations have been made in the shallow seagrass beds adjacent to Padre Island in the Lower Laguna Madre of Texas.

Vegetative fragments were transported in plastic bags to the Plant Ecology Research Laboratory in Austin and planted in 500-ml plastic cups filled with fine sandy loam of Central Texas origin. The cultures were placed in aquaria with artificial seawater (Instant Ocean) and maintained in a greenhouse (with semi-controlled temperatures and controlled day lengths) and in growth chambers (with controlled temperatures and day lengths). Plugs of sod from Redfish Bay were used in some studies. All of the temperatures reported are for water conditions.

The culture studies were conducted with different types of artificial seawater during the 13-year investigation. Originally, the salts were available from the supplier of Instant Ocean in a 2-part combination with some of the nutrients (including chelated iron, copper and zinc) in a trace elements solution. In 1977, all of the ingredients were included in a 1-part salt mixture. Because flowering of *H. engelmanni* was more reliable in the laboratory before 1977, a comparison of the flowering in the two salt combinations was conducted in 1978.

RESULTS AND DISCUSSION

Flowering in Texas Bays

Observations that have been continued at intervals from 1973 to 1985 indicate that flowering of *H. engelmanni* in Texas bays occurs from late April through mid-June. From November 1973 through September 1974, the monthly phenological records in Redfish Bay indicated that flowers first appeared in late April and that both staminate and pistillate flowers were abundant on 4 May and 18 May but that only a few pistillate flowers were noted on 13 June. As indicated by McMillan (1976), some patches were exclusively pistillate or staminate and other patches contained intermixtures. No flowers were observed during the monthly observations from July through September 1974 (McMillan 1976). Observations in 1975 indicated no flowers were evident in February, March, July or November, but those in 1976 indicated that flowers were present in late April and May. Both staminate and pistillate flowers in early stages of development were observed on 25 April 1976. All stages of development for staminate flowers from those in bud to those with tepals open and pollen being shed along with pistillate flowers in various stages of development were observed on 15 May 1976, but no flowers were present in the seagrass bed on 15 July 1976. Observations that were recorded in Redfish Bay in 1981 and in 1983 indicated that both staminate and pistillate flowers were abundant in May.

In 1985, a few staminate and pistillate flower buds in early stages of development were observed in mid-April, but both staminate and pistillate flowers in various stages of development, including anthesis, were observed on 30 April and 9 May (Figs. 1, 2). Additional observations in Lower Laguna

FIG. 1. Reproductive shoots of *Halophila engelmanni* with flowers in various stages of development in Redfish Bay, Texas, on 9 May 1985. Left to right, staminate flower bud emerging from bracts, staminate bud raised above bracts, staminate flower with tepals separated.

FIG. 2. Flowering shoot of *H. engelmanni* in Redfish Bay on 9 May 1985, showing staminate flower with reflexed tepals after release of pollen.

Madre in shallow seagrass beds adjacent to Padre Island in 1980 and 1985 indicated abundant staminate and pistillate flowers in early May. The details of flowering time that were presented for Florida (Short and Cambridge 1984) in 1982 and 1983 indicated that it was similar to that in Texas, and although phenological data were not recorded each year in Texas, it is possible that *H. engelmanni* usually flowers in April–June.

Flowering in an Outdoor Transplant Tank at Port Aransas, Texas

Flowering of three patches of *H. engelmanni* in a large outdoor cement tank at the Marine Science Institute of The University of Texas at Austin was monitored in 1975. On March 20, staminate flower buds were conspicuous on one of the patches and pistillate flowers were present on the other two patches. As indicated above, no flowers were in evidence at the study site in Redfish Bay in March of 1975 (or in March of any other year when observations were recorded). The *H. engelmanni* patches grew from rhizomes (or seed) in sods of *Thalassia testudinum* Banks ex Konig and *Halodule wrightii* Aschers. that were transplanted from Redfish Bay in August 1974 by a summer field course under the supervision of R.C. Phillips (personal communication, 1974). The earlier flowering of *H. engelmanni* in the transplant tank compared to that in Redfish Bay is possibly the result of an earlier appearance of warm temperatures in the tank. Although the temperatures were not monitored continuously, the water in the tank tended to show earlier warming in a comparision of seagrasses from Panama, Belize and Texas (McMillan 1979). The difference in the timing of flower production in the transplant tank and in the natural seagrass beds of Redfish Bay could not be attributed to differences in day length.

Flowering in an Outdoor Transplant Tank at Austin, Texas

Staminate flowers were produced by a sod of *H. engelmanni* that was transplanted from Redfish Bay to Austin in 1981. The time of flower production, 11–21 May, coincided with the time of flowering in Redfish Bay, but the appearance of the first flower buds was approximately two weeks later than the usual dates in the natural habitats (only pistillate flowers, however, were observed at the study site in Redfish Bay on 2 May 1981, but both staminate and pistillate flowers were abundant on 20 May). The sod was removed from the Redfish Bay study site on 30 January and was included with those of *Halodule wrightii* that were studied for reproductive physiology by McMillan (1982). The flowering of *H. engelmanni* in the outdoor tank coincided with warming temperatures: water temperatures were mostly below 22°C in April (except 25°C on 17 April, 26°C on 29 April and 30 April) but increased to 23–24°C in early May. Flower production by the staminate plant ceased as the water temperatures ranged upward between 26–32°C in late May and June.

Flowering Under Controlled Conditions

In 1972, as briefly mentioned by McMillan (1974), two of three replicates of one clone produced staminate flowers and one replicate of each of two other clones produced pistillate flowers under greenhouse conditions (with semi-controlled temperatures and constant 14-h light periods) by mid-March for January transplants. Staminate flowers were also produced under 16-h light periods but no flowers were produced under 12-h light periods as indicated by McMillan (1974). Flowering did not continue under any light period as the temperatures elevated in the greenhouse under late spring and summer conditions. Material that was transplanted in late March and in late July did not produce flowers subsequently during 1972 in the greenhouse, but flowers appeared in January 1973.

To test the effect of continuous light on flowering, vegetative material was transplanted to the Austin greenhouse from Redfish Bay in 1973. For material placed under continuous light on 20 January, pistillate flowers appeared initially on 21 March and five of six replicates had pistillate flowers by 10 April. Additional material that was collected in Redfish Bay in mid-April did not flower until 5 January under the continuous light with four of the eight replicates producing pistillate flowers. In later studies with other seagrasses (*Syringodium filiforme* Kutz., McMillan 1980; *Thalassia testudinum*, Phillips, McMillan and Bridges 1981; *S. isoetifolium* (Ashers.) Dandy, *T. hemprichii* (Ehrenb.) Aschers., *Cymodocea serrulata* (R.Br.) Aschers. & Magnus, *C. rotundata* Ehrenb. & Hempr., *Halodule wrightii*, *H. uninervis* (Forsk.) Aschers., *Halphila ovalis* (R.Br.) Hook.—*H. minor* (Zoll.) den Hartog, McMillan 1982) it has been shown that most, if not all, tropical seagrasses will produce flowers under continuous light if the temperatures are compatible with floral induction.

Although staminate flowers were produced in the laboratory during each of several years, pistillate flowers were produced with greater frequency. Among 16 replicates that were transplanted from Redfish Bay in late February 1974, flowering was observed in late March under 22–24°C and 14-h light periods. Five of the replicates produced both staminate and pistillate flowers, but in each the staminate flower production was confined to April and pistillate flower production was March–June. A total of 29 staminate and 37 pistillate flowers were produced by the five replicates; 82 pistillate flowers were recorded on the other 11 replicates. The greater frequency of pistillate flowers in the cultures has been characteristic of other species of *Halophila* (McMillan 1983).

Vegetative material that was moved from Redfish Bay on 27 June 1974 was induced to flower subsequently in the laboratory under controlled conditions (McMillan 1976). Nine replicates were initially kept at 22–24°C and 14-h light periods and then divided among three temperatures: 27.5°, 23.5° and 17.5°C. The first pistillate flower appeared in a culture at the highest temperature on 31 August and each of the three replicates at 27.5°C had pistillate flowers by 23 October, but no new flowers appeared subsequently

at this temperature. Two of the three replicates at 23.5°C produced pistillate flowers almost continuously from October through January. No flowers were produced by the three replicates at the lowest temperature, 17.5°C, but pistillate flowers were produced after the cultures were moved to 27.5°C.

To examine a difference in flowering that was noticed among cultures between 1976 and 1977, the possible effect of the seawater was examined. Plants collected in July 1976 and kept at 22–24°C were with flowers on 21 August, eight of 18 replicates with pistillate flowers, but plants collected in June 1977 did not flower subsequently in the laboratory. Because the seawater in 1976 had been prepared with the 2-part combination available in Instant Ocean products and that in 1977 from 1-part Instant Ocean salts, the difference in flowering between 1976 and 1977 possibly resulted from the difference in the seawater. For a comparison, 24 replicates that were collected in Redfish Bay on 18 December 1977 were placed at 24°C and 14-h light periods in aquaria containing seawater of different composition. In February 1978, 7 of the 12 replicates in the 2-part salt mixture (Prepared with the salts only and without the liquid second part) had flowers, but on the same date, only one of the 12 in seawater synthesized from the 1-part salt mixture had flowers. A difference in flowering that appears to be related to the seawater, with flowering being more reliable in the 2-part salt mixture available from Instant Ocean before 1977, has been demonstrated also for *Syringodium filiforme* (McMillan 1980) and for *S. isoetifolium*, *Halodule wrightii* and *H. uninervis* (McMillan 1982).

As indicated in McMillan (1976), flowering in *H. engelmanni* is inhibited at lower salinities. Plants kept at 10 and 18‰ did not flower but did so after a transfer to salinities from 21 to 35‰. Observations both in the laboratory and in the field indicate that sudden changes in the salinity to reduced levels affect the vegetative and flowering status of *H. engelmanni*. Following heavy rains, the plants in Redfish Bay show deterioration of the leaves and the flowers and produce new leaves from buds under the sediment. Similarly, most leaves on the vegetative transplants to the laboratory deteriorate and are replaced by new leaves that rapidly enlarge from the buds.

Effects of Temperature and Photoperiod

Although McMillan (1976) suggested that the flowering time of *H. engelmanni* was correlated with temperatures between 22 and 27.5°C, he indicated that flowers might be inhibited by the shorter daylengths of winter. The photoperiod sequence at both Ft. Pierce, Florida, and Port Aransas, Texas, is nearly identical because of the similarity of latitude and is approximately 13 h (including civil twilight to which plants react before sunrise and after sunset) in mid-March lengthening in June to 15 h. Short and Cambridge (1984) indicated that the longest photoperiod at Ft. Pierce was 14 h (without the civil twilight) and reported temperatures of 24–29°C during flowering in 1982 and a 3–5°C warmer condition in 1983. Because

they did not detect a difference in flowering time between 1982 and 1983, they concluded that photoperiod was the critical factor controlling flowering time. However, as indicated above, the earlier flowering (in late March) in a transplant tank at Port Aransas, separated by a few miles from the Redfish Bay site, could not be attributed to a difference in day length. Under the lengthening days of March and April, the key factor in the timing of reproductive activity is the warming of the water temperature during spring.

The effects of high temperature on *Halophila* have been published recently (McMillan 1984). Among the seagrasses, *H. engelmanni* is one of the most sensitive to high temperature stresses. Replicates of *H. engelmanni* that were in mixed sods with *Halodule wrightii* from Redfish Bay withstood only 1 h at 39°C, but those of *H. wrightii* withstood up to 120 h at this temperature. Although *H. engelmanni* is common in shallow seagrass beds with *H. wrightii* it is a less permanent resident of near inshore sites. The demography of the *H. engelmanni* population at the Redfish Bay site has been altered repeatedly during the 1972–1985 observations as a result of silting and possibly as a result of high temperature stresses. Staminate and pistillate plants have occupied different microsites but have been observed continuously through 1985 near the original sites reported in 1972.

Description of Staminate Flowers

The description of staminate flowers of Redfish Bay, Texas (McMillan 1976) differs in some respects from the details of a flower from Florida illustrated by Short and Cambridge (1984). The staminate flowers of Texas were described as having tepals that were 4–5 mm long and 2.5–3.0 mm wide (McMillan 1976). No measurements were given for the tepals of the Florida flower, but those that are shown on the illustration (Short and Cambridge 1984) appear to be *ca.* 5 mm long and 1.8 mm wide (as indicated by a scale bar accompanying the illustration). The stamens were described for the Texas flowers as *ca.* 3 mm long and those for the Florida flower as 4 mm long. The staminate flowers from Redfish Bay (Fig. 2, 3) show the wider tepals and shorter stamens that are characteristic of the Texas populations. The possible differences between flowers of *H. engelmanni* of Texas and those of Florida will need to be studied further to determine if there are populational differences within the species with respect to flower size as has been shown for leaf morphology for Texas plants and those of the Gulf of Mexico coast of Florida (McMillan 1978).

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FIG. 3. Staminate flower in 1976 laboratory culture from Redfish Bay showing linear tetrads of pollen in gelatinous sheaths. Photographed with reflected light to show convex tepal.

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